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STATE-PROTECTED RARE SPECIES IN CALIFORNIA

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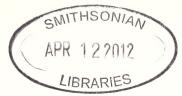
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### RECONSIDERATION OF THE TAXONOMIC STATUS OF MASON'S LILAEOPSIS – A STATE-PROTECTED RARE SPECIES IN CALIFORNIA

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#### ABSTRACT

Lilaeopsis masonii is a California state-listed rare species with a wide range of morphologies observed in the field throughout its range, and in herbaria collections. This extensive variation confounds reliable taxonomic identification, particularly for those specimens intermediate between L. masonii and its sister taxon, L. occidentalis. To investigate the genetic basis of this morphological variation, we examined two portions of the *Lilaeopsis* genome in seven species. Specifically we sought to determine whether L. masonii is sufficiently distinct from its closely related, widespread congener to continue to warrant specific status. DNA sequence analysis of ITS1, 5.8S, and ITS2 nuclear ribosomal DNA revealed no differences between L. occidentalis and L. masonii California collections, and minimal differences between these samples and L. occidentalis collected from the state of Washington, suggesting strongly that these two species form a single clade. A combination of fragment data from three AFLP primers yielded 274 fragments from 29 samples. Genetic Manhattan distance values calculated from the AFLP matrix within species ranged from a low of 1.4 to a high of 6.6, reflecting minor differences among all samples. UPGMA cluster phenograms support the results of the PCA analysis, illustrating a cluster of L. occidentalis + masonii samples distinct from other Lilaeopsis species. Because conservation dollars should protect unique evolutionary entities, we suggest that L. masonii be subsumed under L. occidentalis and therefore no longer receive formal state protection.

Key Words: AFLP, Apiaceae, California endangered species Act, goldilocks conundrum, ITS, lilaeopsis masonii, lilaeopsis occidentalis, UPGMA.

Lilaeopsis masonii Mathias & Constance (Mason's lilaeopsis) is one of 15 wetland or aquatic species of the widespread genus Lilaeopsis Greene within the Apiaceae. The genus Lilaeopsis is comprised of perennial herbs characterized by a horizontal stem with leaves commonly in clusters ("ramets") borne directly from the stem, although rarely leaves occur individually. Lilaeopsis is notable in its morphologic simplicity—entire, generally linear leaves; simple umbels; absence of a carpophore; and, a strongly reduced habit (Petersen et al. 2002; Downie et al. 2000; Downie et al. 2008). Such simple morphology has led to a long history of taxonomic uncertainties and difficulty in the reconstruction of its phylogeny.

Evidence for monophyly of *Lilaeopsis* is strong (Petersen et al. 2002). However, recent research based on molecular evidence from nuclear and chloroplast genes suggests that the genus is best placed in the Oenantheae tribe within the Apioideae (Downie et al. 2008) and that *Lilaeopsis* is sister to the clade comprising *Ptilimnium*, *Limnosciadium*, *Daucosma*, *Cynosciadium* and rachis-leaved species of *Oxypolis*, not the Mexi-

can genus *Neogoezia* as suggested by Petersen et al. (2002). The New World endemics clade of tribe Oenantheae is native to North America and comprises a monophyletic group that appears to be evolving much faster than any other major clade recognized in the tribe (Hardway et al. 2004).

Early taxonomic work on the genus in California by Hill (1927) and Mason (1957) included mention of comparatively smaller and narrower leaves in Lilaeopsis specimens occurring away from the coast, in contrast to a relatively more robust coastal form. Professor Herbert Mason, an early expert on the wetland flora of California, first collected a relatively smaller Lilaeopsis from Brannan Island of the San Francisco Bay/Sacramento-San Joaquin Delta (Bay-Delta). He referred to the smaller form as the "San Francisco Bay and river-mouth" form (Mason 1957: 631). This specimen, according to Mason (unpublished) was "definitely distinct from the coastal L. occidentalis." Western lilaeopsis (Lilaeopsis occidentalis J. M. Coulter & Rose) is a widespread, common species,

ranging from the Queen Charlotte Islands of British Columbia, Canada to Marin County, California (Affolter 1985). Considered to be a coastal species confined to salt water or brackish water intertidal habitats, collections of *L. occidentalis* from inland fresh water lentic and lotic habitats are known, but considered "uncharacteristic" (Affolter 1985).

Lilaeopsis masonii was not described as a distinct taxon for two decades after the smaller form in the Bay-Delta was first observed. In 1977, Mathias and Constance formally recognized the diminutive nature of a specimen obtained from Twitchell Island in the Bay-Delta as L. masonii (Mathias and Constance 1977). Mathias and Constance described L. masonii as distinct from L. occidentalis based upon the former (rare) taxon bearing narrower, typically shorter, and more or less terete leaves, and an inland distribution. They honored Herbert Mason's expertise in the wetland flora of the State with the specific epithet.

Mason's lilaeopsis was one of the first vascular plant species to be protected as "rare" under the California Endangered Species Act (CESA) (California Fish & Game Code §§2050, et seq.). At the time of its listing in November 1979, only seven population occurrences were known (CNDDB 2009). Since formal protection, the documented extent of geographic distribution and population abundance of L. masonii has increased nearly three-fold, primarily as a result of concentrated field survey efforts conducted in the early 1990's by Golden, Fiedler, and Zebell (Golden and Fiedler 1991; Golden 1992; Fiedler and Zebell 1993; Zebell and Fiedler 1996). Today, Mason's lilaeopsis is known to occur within 24 USGS quadrangles and seven counties (CNPS 2008), spanning across roughly 690 square miles. One hundred eighty-six documented occurrences are on record with the state (CNDDB 2009), although most, but not all are extant.

### A History of Taxonomic Uncertainty

Confusion over the taxonomic limits of this rare species existed from the beginning of its description. Two examples are relevant. First, a long-controversial *Lilaeopsis* specimen collected by Schreiber (#2266 UC, 28 June 1936) from Chicken Ranch Beach in Marin County derives from outside the circumscribed geographic range of the endemic inland taxon. Leaf lengths from this specimen range between 15 to 42 mm, a morphological range characteristic of comparatively larger leaf lengths for *L. masonii*. However, it is possible to key these larger leaved Chicken Ranch Beach specimens to *L. occidentalis* in every relevant flora (e.g., Hickman 1993).

Affolter (1985) examined this specimen in his monograph of *Lilaeopsis*, and accepted it as *L*.

masonii, but noted that it was a geographical outlier for the rare, Bay-Delta endemic species. Today, CNPS (Tibor 2001) acknowledges that this specimen is likely to be *L. occidentalis*, not the rare *L. masonii*, but provides no explanation. Several attempts to relocate this *Lilaeopsis* material at Chicken Ranch Beach by the authors have failed as the population appears to be extirpated, thereby making an independent species corroboration impossible.

It is important to note that (1) numerous collections of *L. occidentalis* from the beaches of Marin and Sonoma counties exist, (2) leaf lengths range by an order of magnitude or more within and between adjacent populations of *L. occidentalis*, (3) the number and clarity of internal crosswalls considered important diagnostic characters are more likely a function of relative plant size, exposure, or both, and (4) inland collections of the common species are known from the state of Washington (e.g., UC 1594452; 4 September 1962). Also noteworthy, *L. masonii* has never again been collected on the Pacific coast of North America beyond Schreiber's Marin Co. collection in 1936.

Further, Affolter (1985) remarked that leaves from a collection of *L. masonii* (derived from Sherman Island immediately down river of Twitchell and Brannan islands) cultivated for his greenhouse comparisons were "remarkably longer than any of the herbarium material" (Affolter 1985:70). He suggested the observed overall larger and more robust greenhouse material was evidence of how difficult it is to understand vegetative plasticity from herbarium material alone. However, the relatively robust response of Mason's lilaeopsis to the mild conditions of a greenhouse suggests strongly that strict morphological distinctions between the two taxa are problematic.

Additional morphological characters further support the assertion that *L. masonii* is not distinctly different from *L. occidentalis*. Affolter (1985:70) noted that the "two taxa are similar in several respects," including similar (1) leaf shapes (linear), (2) rhizome branching architecture, (3) fruit shapes, (4) fruit cell types, (5) fruit venation patterns, (6) habitats, and they have (7) overlapping geographic distributions. Despite all these similarities, Affolter (1985:71) supported their separate specific status, primarily because "when grown under a common-garden environment in the greenhouse, the two species retained the vegetative characteristics that distinguish them in the field."

Subsequent laboratory studies conducted by the principal author and her students (Golden and Fiedler 1991; Golden 1992; Fiedler and Zebell 1993; Zebell and Fiedler 1996) have provided little clarity. Most importantly, no nucleotide variation was found among nine populations of *L. masonii* or between *L. occidentalis* and *L. masonii* when the 204 nucleotides of the ITS2 nuclear genome were ascertained (Fiedler and Zebell 1993). Fiedler and her colleagues thus concluded tentatively that the rare species was most likely an inland ecotype not clearly distinct from its widespread congener.

### Field Observations

Decades of field observations of Lilaeopsis throughout the Bay-Delta, Suisun Marsh, and Napa River ecosystems do not reinforce many of the conclusions offered by Hill (1927), Mason (1957, unpublished), Mathias and Constance (1977), and Affolter (1985) supporting the recognition of two distinct taxa. Rather, the few vegetative characteristics that typify this genus are highly variable both within and between populations throughout this region. Occurrences of L. masonii in the lower Napa River, studied since 2001 (WSP 2007, unpublished; Blasland, Bouck, & L, Inc. unpublished; Entrix unpublished; L.C. Lee & Associates unpublished; Stillwater Sciences and Fiedler unpublished) include a full spectrum of individual ramet sizes. Often, both large and small forms of *Lilaeopsis* species, easily identifiable to the two different species, can be found growing in the same location. Often the plant stature/leaf length size gradient runs perpendicular to the shoreline, where the small 'masonii' form (approx.1.5-4.5 cm in height) grows relatively close to the water's edge, while increasing larger and more robust "occidentalis" (approx. ≥11 cm in height) can be found further from the water. "Intermediate" or medium-sized Lilaeopsis material (approx. >6.25 and <11 cm in height) is common throughout this shoreline/ river bank habitat and geographic range, and keys to either (or both) the rare or the common species. We call this phenomenon—i.e., range in size of a critical morphological character, with significant overlap between taxa—the "Goldilocks Conundrum" to highlight the problem that the intermediate-sized material is not "just right," but rather, highly problematic.

To resolve our conundrum and determine whether *L. masonii* is a discrete species distinct from *L. occidentalis*, we initiated a genetic analysis of seven species of this genus. We hypothesized that there were no significant differences between diagnostic portions of the genome selected for this study of the two species, *L. masonii* and *L. occidentalis*. Based on these analyses, we then explored whether *L. masonii* warrants continued recognition as a distinct species or rather, should be subsumed under the widespread and common *L. occidentalis*. If no significant differences were shown to exist between diagnostic portions of the *L. occidentalis* and *L. masonii* genomes, then *L. masonii* should

be subsumed within *L. occidentalis*, and continued protection under the California Endangered Species Act for *L. masonii* should be reconsidered.

Fallon (2007) noted that genetic information is being used increasingly to resolve taxonomic issues for protection at the federal level under the U.S. Endangered Species Act of 1973 (ESA). She conducted a review of listing decisions made by the U.S. Fish & Wildlife Service and the National Marine Fisheries of species, subspecies, or distinct population segments (DPSs) proposed for protection under the ESA. Fallon determined that the listing fate of a DPS based upon data from more than one genetic marker resulted in a higher probability of protection than candidate taxon or population segment whose discreteness was determined by a single genetic marker. With the cautionary tale of Fallon's findings in mind, we examined the ITS region of the nuclear genome and, to corroborate our ITS findings, conducted an amplified fragment length polymorphism (AFLP) analysis on a similar suite of taxa.

We chose the ITS region in large part because Hardway et al. (2004) found evidence for particularly rapid evolution in the *Oenanthe* clade that includes Lilaeopsis when compared to the rest of the taxa. Sequence divergences in this clade averaged 6–7 times higher (approx. 17%) than between species in *Oenanthe* (approx. 2.8%) or Cicuta (approx. 2.4%) (Hardway et al. 2004). AFLP analysis was selected as a secondary marker system based on the increasing popularity of this form of DNA fingerprinting as a complementary system in phylogenetic studies (Holland et al. 2008). Additionally, AFLP fingerprinting offers a reliable, robust, and genomically comprehensive method of genetic analysis for taxa lacking complex nuclear and organellar markers (Vos et al. 1995).

### MATERIALS AND METHODS

### Field Collection

Lilaeopsis masonii specimens were collected in the spring of 2007 from locations along the Napa River and in the Sacramento/San Joaquin Delta. Lilaeopsis occidentalis was collected from Bodega Head, California, and Mason and Lawrence lakes in Washington State (Fig. 1). Leaf material to be used in DNA extraction was preserved in silica gel at the time of collection. Vouchers were deposited at the herbarium at San Francisco State University (SFSU) (Table 1). Material for L. brasiliensis (Glaz.) Affolter and L. mauritiana G. Petersen & J. Affolter was obtained from a commercial aquarium supplier (freshwateraquariumplants.com). The dataset is composed of 35 nrDNA ITS sequences representing seven taxa, including three sequences

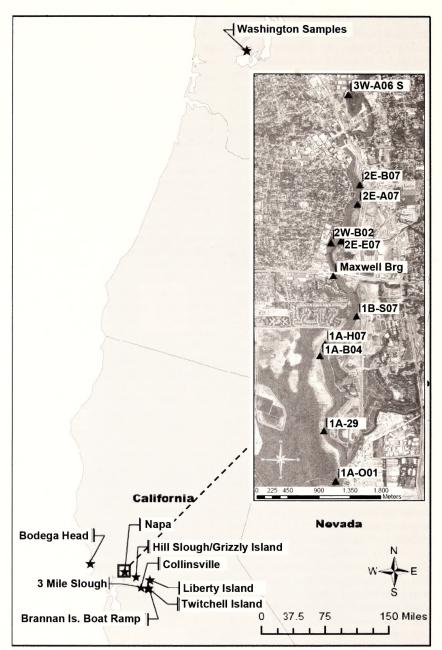


FIG. 1. Map of the geographic locations of Lilaeopsis masonii and L. occidentalis specimens collected for this study.

from Genbank (*L. carolinensis* J. M. Coulter & Rose, *L. novae-zelandiae* (Gand.) A. W. Hill, and *L. occidentalis*), two specimens from the aquarium trade labeled as *L. brasiliensis* and *L. mauritiana*, and two specimens of *L. schaffneriana* (Schltdl.) J. M. Coulter & Rose subsp. *recurva* (A. W. Hill) Affolter courtesy of the Desert Botanical Garden staff. Comprehensive sampling was conducted for *L. masonii* and *L. occidentalis* as the purpose of this study was to resolve the taxonomic classification for these two species. A detailed systematic

study for *Lilaeopsis* is in preparation (S. Downie, Univ. of Illinois, Urbana-Champaign, personal communication).

### ITS Methods

DNA from leaf tissue of five of the seven species was extracted using the Qiagen DNeasy Plant Mini Kit (QIAGEN, Inc., Valencia, CA), following the manufacturer's protocol with slight modifications. *Lilaeopsis carolinensis* and *L*.

TABLE 1. COLLECTION INFORMATION AND GENBANK ACCESSION NUMBERS FOR ITS AND AFLP ANALYSES.

| Species                          | Sample location / GenBank reference no.   | County, state  | UTM                      | EASTING   | NORTHING   | Date collected  | Voucher location                                     |
|----------------------------------|---|--|--------------------------|---|--|---|--|
| L. carolinensis                  | ITS: EF17713  | NA   | NA                       | NA  | NA   | NA  | Argentina, cult.<br>Univ. of Mich<br>Botanic Gardens |
| L. masonii                       | Napa River 1A-29a Napa River 1A-29b Napa River 1A-9b Napa River 1A-B04 Napa River 1A-H07a Napa River 1A-H07b Napa River 1A-H07b Napa River 1B-807 Napa River 2E-A07 Napa River 2E-E07a Napa River 2E-E07a Napa River 2E-E07b Napa River 2E-E07b Napa River 2W-B02a Napa River 2W-B02b Napa River 3W-01/HQ647239 Napa River 1A-O01/E02 Napa River 1A-O01/H #HQ647245 Brannan Island boat ramp -003 //# #HQ647245 Brannan Island boat ramp -003 //# #HQ647245 Collinsville-007 //# HQ647238 Hill Slough/Grizzly Island-006 //# HQ647242 | Napa, CA Sacramento, CA Solano, CA Solano, CA |                          | 0562369<br>0562369<br>0562318<br>0562303<br>0562379<br>0562379<br>0562510<br>0562611<br>0562611<br>0562463<br>0562463<br>0562463<br>0562463<br>0562463<br>0562463<br>0562463<br>0562463<br>0661393<br>0613933<br>0613935<br>0613939 | 4234924<br>4234924<br>4236035<br>4236101<br>4236283<br>4236283<br>4237260<br>4237266<br>4237766<br>4237766<br>4237766<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4237739<br>4218528<br>4218528<br>4218528<br>4218528<br>4218538<br>4218538<br>4218538 | \$/6/2007<br>\$/8/2007<br>\$/9/2007<br>\$/9/2007<br>\$/8/2007<br>\$/10/2007<br>\$/10/2007<br>\$/25/2007<br>\$/24/2007<br>\$/24/2007<br>\$/24/2007<br>\$/24/2007<br>\$/24/2007<br>\$/24/2007<br>\$/24/2007<br>\$/24/2007<br>\$/24/2007<br>\$/24/2007<br>\$/24/2007<br>\$/24/2007<br>\$/24/2007<br>\$/24/2007<br>\$/24/2007<br>\$/24/2007<br>\$/24/2007<br>\$/24/2007<br>\$/24/2007<br>\$/24/2007<br>\$/24/2007 | SFSU SFSU SFSU SFSU SFSU SFSU SFSU SFSU              |
| L. novae-zelandiae               | ITS:AF466278  | N/A  | N/A                      | N/A   | N/A  | N/A   | New Zealand, cult.                                   |
| L. occidentalis                  | Bodega Head // #HQ647236<br>Mason Lake, WA //# HQ6472344<br>Lake Lawrence, WA //# HQ647243<br>ITS:AY360242  | Marin, CA<br>Mason, WA<br>Thurston, WA<br>N/A  | 11S<br>10T<br>10T<br>N/A | 0494826<br>0503357<br>0503357<br>N/A  | 4231320<br>5241674<br>5188743<br>N/A   | 10/7/2007<br>7/25/2008<br>7/25/2008<br>N/A  | SFSU<br>SFSU<br>SFSU<br>SFSU<br>USA, Oregon,         |
| L. schaffneriana                 | Scotia Canyon, Arizona //# #HQ647231<br>Scotia Canyon, Arizona //# HQ647232   | Cochise, AZ<br>Sonoita, AZ   | N/A<br>N/A               | Approx. 557009 Approx. 526984   | Approx.<br>3479631<br>Approx.<br>3501690   | 6/14/1991   | SFSU SFSU  |
| L. brasiliensis<br>L. mauritiana | Freshwateraquariumplants.com //# HQ647234<br>Freshwateraquariumplants.com //# HQ647233  | N/A<br>N/A   | N N A A                  | N/A<br>N/A  | N/A<br>N/A   | N/A<br>N/A  | SFSU<br>SFSU   |

TABLE 2. AFLP PRIMER AND ADAPTER SEQUENCES.

| Primer     | Sequence                    |
|------------|-----------------------------|
| Ad1EcoRI   | 5' -CTCGTAGACTGCGTACC- 3'   |
| Ad1MseI    | 5' -GACGATGAGTCCTGAG- 3'    |
| prampEcoRI | 5' -GACTGCGTACCAATTCA- 3'   |
| prampMseI  | 5' -GATGAGTCCTGAGTAAC- 3'   |
| FAM-EcoRI  | 5' -GACTGCGTACCAATTCAAC- 3' |
| HEX-EcoRI  | 5' -GACTGCGTACCAATTCACG- 3' |
| MseI + CAA | 5' -GATGAGTCCTGAGTAACAA- 3' |
| MseI + CAT | 5' -GATGAGTCCTGAGTAACAT- 3' |
| MseI + CAG | 5' -GATGAGTCCTGAGTAACAG- 3' |

novae-zealandiae were excluded from this analysis due to technical difficulties with the DNA extraction from the leaf material. Dilutions of the genomic DNA extract of 1:10 in ultrapure water were used in PCR reactions. The contiguous ITS1, 5.8S, and ITS2 regions of nuclear ribosomal DNA were PCR-amplified using the primers ITSLEU (Baum et al. 1998) and ITS4 (White et al. 1990) in final reaction volumes of 25 μl. Positive amplifications were purified using the MO BIO UltraClean PCR Clean-up DNA Purification Kit (MO BIO Laboratories, Inc., Solana Beach, CA). Internal primers ITS2 and ITS3 (White et al. 1990) were used in addition to ITSLEU and ITS4 in cycle-sequencing reactions in order to extend fragments and clarify ambiguities. Fragments were sequenced with the BigDye 3.1 kit (Applied Biosystems, Foster City, CA) following the manufacturer's protocols, and visualized using the ABI PRISM 3100 Genetic Analyzer (Applied Biosystems). Sequences were manually aligned using Sequencher 3.1.1 (Gene-Codes Corp., Ann Arbor, MI) and MacClade 4.04 (Maddison and Maddison 2001).

### AFLP Methods

AFLP fingerprinting was conducted following a modified protocol based on the methods described by Vos et al. (1995). DNA extracts prepared for ITS analysis also were used for this study undiluted. Approximate DNA concentrations for all samples were estimated to contain a range of concentrations from 10 ng/µl to 50 ng/µl using an ethidium dot test. DNA template of each sample was digested using the infrequent endonuclease cutter *EcoR1* and the frequent endonuclease cutter *MseI*. Immediately following digestion, the entire digestion reaction was combined with an equal volume of ligation mix.

The resulting fragmented DNA template containing "sticky ends" was diluted five-fold and subsequently amplified by PCR using a preselective primer mix. This step effectively reduces the number of possible fragments by approximately 1/16<sup>th</sup> (Meudt and Clarke 2007). The

pre-selective reaction condition consisted of 30 cycles of 94° for 30 sec, 56° for 1 min, and 72° for 1 min.

Three combinations of selective primer sets were used to produce a final AFLP fingerprint for each sample (Table 2). Each set of selective primers consisted of a primer region matching the known adapter sequence, as well as three selective nucleotides on the 3' end of the MseI primer and three selective nucleotides plus a florescent label on the 3' end the of EcoRI primer. Template for the pre-selective PCR was diluted 6-fold and then combined with a master mix containing one set of selective PCR primers. A step-down PCR was used to amplify the selective fragments in a program consisting of 13 cycles of 94° for 30 sec,  $65^{\circ}$  for  $30 \sec (-0.7^{\circ} \text{ per cycle})$ , and  $72^{\circ}$  for 1 min, followed by 24 cycles of 94° for 30 sec, 56° for 30 sec, and  $72^{\circ}$  for 10 sec.

The final selective PCR product fragments containing a fluorescently labeled *Eco*RI end and unlabeled *Mse*I end were analyzed undiluted using an ABI 3100 genetic analyzer (Applied Biosystems). Initial fragments were sized first using the analysis software GeneScan (Applied Biosystems) and using the program by GeneMarker<sup>®</sup> (SoftGenetics, State College, PA). After a comparison of fragment calling using both programs, all samples were analyzed using GeneMarker<sup>®</sup>.

Fragments were recorded for each sample in a data matrix based on a binary system (1 for presence, 0 for absence); a data matrix was developed for each primer combination and then all data was collated into a single data matrix. To test reproducibility of results, twenty percent of all samples selected at random for each primer pair were re-analyzed, starting with the initial DNA extracts. Fragment peaks that were determined to be consistently low (below 300 peak intensity) or unpredictable were dropped from the matrix table.

### Data Analysis

Phylogenetic analyses of ITS sequences were conducted using Phylip version 3.68 (Felsentein 2004). All characters were weighted equally,

character state transformations were treated as unordered, and gaps were treated as missing data. Most-parsimonious trees were obtained in Phylip using the "branch-and-bound" method of exact search implemented by the analysis unit DNA-PENNY. Bootstrap re-sampling (1000 replicates) was used to assess nodal support (Felsenstein 1985). Most parsimonious trees were generated from a search of 100,000 trees and a final tree was derived using a strict consensus tree method (Felsenstein 2004). Additional tree searches were conducted in greater volumes, up to 1,000,000. However, larger searches produced the same final tree, thus a smaller tree search was selected to reduce run-time during bootstrapping. Several combinations of Lilaeopsis species outgroups were explored before selecting L. novae-zelandiae as the outgroup. This selection was based on indications of a potential sister group relationship between L. novae-zelandiae and L. occidentalis, which was supported by ITS phylogenetic analysis of this genus within the Apiaceae tribe described in Downie et al. (2008). Genetic distances to determine branch lengths were calculated in Phylip using the Jukes-Cantor method implemented in DNADIST and a Fitch-Margoliash (FITCH) search.

AFLP phylogenetic analysis was performed using the program Phylip version 3.68 (Felsenstein 2004). A genetic distance matrix was created using the techniques described by Nei and Lei (1979) as implemented by RestDist in Phylip (Felsenstein 2004). The output matrix was then input into NEIGHBOR using the UPGMA method of cluster analysis (Felsenstein 2004). Using this approach, an output tree was constructed by successive clustering using an average-linkage method of clustering. The output file was then plotted as both a rooted and unrooted tree. A search for the most parsimonious trees was implemented first using the branch-andbound algorithm of DOLPENNY (100,000 trees searched) in Phylip following bootstrap analysis using 100 replicates. A 50% majority-rule consensus tree was then generated to condense the results into a final tree, which is presented here. Previous studies of Lilaeopsis using AFLP analysis have not previously been reported. As such, outgroup selection for AFLP parsimony analysis was determined following variable, preliminary analysis replicates. Lilaeopsis schaffneriana was selected as this species is the closest geographically to both L. masonii and L. occidentalis. Further, L. schaffneriana also demonstrated sufficient genetic differences to be used as an appropriate outgroup.

To further visualize potential multi-dimensional correlation of AFLP data based on genetic similarities, an additional genetic distance matrix was derived using Manhattan distance (StatisiXL; www.statistixl.com). These

data were then analyzed using a principal coordinates analysis (PCA) using the Microsoft Excel<sup>®</sup> add-in program GenAlEx 6.2 (Peakall and Smouse 2006). To determine whether a measurable degree of genetic dissimilarity among L. occidentalis (WA and CA samples) and L. masonii (CA samples) could be attributed to geographic distance, an additional test of molecular variance based on geographic origin as measured by Global Position System (GPS) also was tested. A two-way analysis of variance was assessed for collections of L. occidentalis and L. masonii using an analysis of molecular variance (AMOVA) with GenAlEx 6.2 (Peakall and Smouse 2006). Significance was assessed using 99 permutations.

### RESULTS

DNA sequence analysis of the ITS regions ITS1, 5.8S, and ITS2 of nuclear ribosomal DNA, based on a most parsimonious search of 64,631 trees using a branch-and-bound method, revealed no differences between California samples of L. occidentalis and L. masonii samples, including a GenBank accession for L. occidentalis (100 of 100 trees) (Fig. 2). Within the L. occidentalis\L. masonii clade, samples collected from Washington clustered separately. Distance values between Washington and California samples were low for single collections from Lawrence Lake and Mason's Lake (0.1 and 0.3%, respectively). However, a second sample from Lawrence Lake exhibited higher distance values (1.5%), which may be due to missing data. Distance values for California samples of L. masonii and L. occidentalis were 0% across all samples. Comparatively, distance values between the additional species used for this study ranged from 1.2–8%. Distance based analysis of ITS sequences found an identical tree structure as the strict consensus tree inferred from most parsimonious results implemented by DNAPENNY. Bootstrap estimates from 1000 replicate analyses yielded 100% nodal support for all branches. Branch placement and relationship of *Lilaeopsis* species used in this study are consistent with results of a previous ITS phylogenetic analyses by Downie et al. (2008), though that study excluded *L. masonii*.

The three AFLP primer combinations generated 274 unique fragments among 29 samples, with only 21 fragments shared or monomorphic between the five species used in this study. Although a small sample size was used, specifically for *L. brasiliensis*, *L. schaffneriana*, and *L. mauritiana*, the large number of shared fragments is potentially indicative of low genetic diversity within this genus, which is consistent with species exhibiting high morphologic plasticity (Linhart and Grant 1996). The number of total diagnostic bands from the three markers combined data set

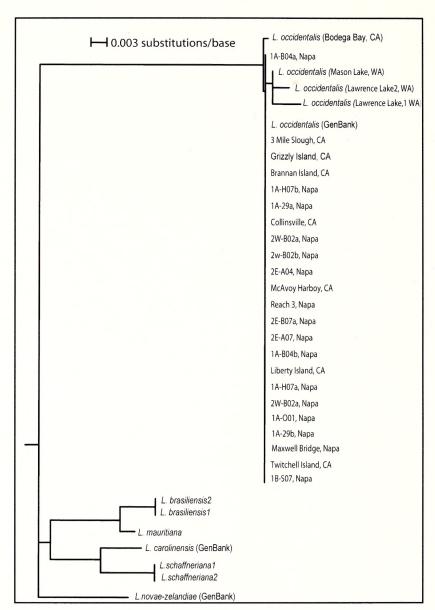


FIG. 2. Strict consensus tree derived from ITS sequence data using the branch and bound method implemented by DOLPENNY. Branch values are Bootstraps. Upper left tree illustrates distance values, branch lengths are proportional to the number of nucleotide substitutions per base.

varied between species, ranging from a low of 98 bands for one sample of L. schaffneriana, to a high of 135 bands for the Mason Lake, WA sample of L. occidentalis, with a mean number of AFLP bands equaling 123 (SD = 9.5) (Table 3).

Within species genetic distance values (Manhattan distance calculated from the AFLP matrix) ranged from a low of 1.4 for *L. masonii* (Napa River site #1A-H07, large and small forms), to a high of 6.6 for *L. masonii* (Napa site 1A-B04 and Twitchell Island collections). Between species values ranged from a low of 4.1 for *L. occidentalis* (Mason Lake, WA) and *L.* 

masonii (Napa River #2W-B02), to high of 11.9 for *L. schaffneriana* and *L. occidentalis* (Lake Lawrence, WA collection).

Principal coordinate analysis (PCA) illustrated an overlapping association between samples of *L. occidentalis* and *L. masonii* (Fig. 3), but a clear differentiation between the *L. occidentalis/L. masonii* cluster and all other *Lilaeopsis* species examined in this study, i.e., *L. schaffneriana*, *L. mauritiana*, and *L. brasiliensis*. The small separation observed between the *L. occidentalis* and *L. masonii* data may be attributed to geographic distance. Results of AMOVA analysis derived

TABLE 3. AFLP FRAGMENT NUMBERS FOR EACH SPECIES.

|                                 | Mean or Total No. of Fragments |      |      |       |  |
|---------------------------------|--------------------------------|------|------|-------|--|
| Species                         | CAA                            | CAG  | CAT  | Total |  |
| L. masonii                      | 53.5                           | 46.1 | 21.9 | 125.1 |  |
| L. occidentalis                 | 52.7                           | 50   | 22.9 | 128.8 |  |
| L. schaffneriana subsp. recurva | 47.5                           | 34.5 | 16   | 99.5  |  |
| L. brasiliensis                 | 52                             | 39   | 21   | 114   |  |
| L. mauritiana                   | 43                             | 38   | 16   | 99    |  |
| All Fragments                   |                                |      |      | 123   |  |

from grouping samples based on geographic location indicated that approximately 73% of genetic variation was distributed between groups and thus 23% among groups, supporting the conclusion that most observed genetic variation is due to geographic distance (P = 0.01).

The UPGMA cluster phenograms provides additional support for the results of the PCA analysis, illustrating a combined grouping of L. occidentalis (CA and WA) and L. masonii samples (Fig. 4). Within the L. occidentalis and L. masonii clade, samples collected from Washington clustered separately from samples collected within California, corroborative of results of AMOVA indicating that variation within this clade is due in large part to geographic distance. Samples of L. brasiliensis and L. mauritiana cluster separately but are sister to the L. occidentalis/L. masonii clade; L. schaffneriana samples also cluster separately but are sister to all other specimens/species used for this study. The most parsimonious tree from the maximum parsimony analysis supports a single L. occidentalis/L. masonii clade; however, additional resolution within this taxon is less certain of the specific placement of *Lilaeopsis* samples, based on geographic location (Fig. 5).

#### DISCUSSION

Taxonomic implications. Within the last two decades, the use of genetic techniques to distinguish discrete evolutionary units has become common place in systematic biology. Use of genetic data in the protection of endangered species when morphological (or other character) information is either unreliable or impossible is just one reason why this approach to species identification and delimitation is so important (Avise 2003). Thus, sole reliance on morphological, geographic, reproductive behavior or some combination of non-genetic characters to delimit taxa is no longer defensible when diagnostic genetic information is available and can be readily assessed. In the case of Lilaeopsis masonii and L. occidentalis, neither ITS sequence nor AFLP fragment length data support the recognition of the *L. masonii* as a distinct evolutionary entity.

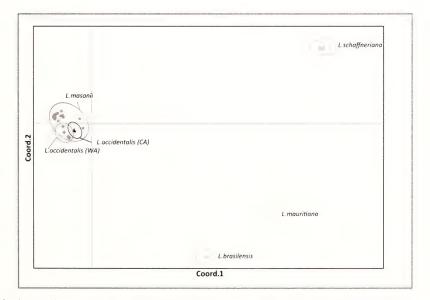


FIG. 3. Principal coordinates analysis (PCA) of AFLP fragment data matrix. Codes for Napa collections, e.g., 1A-H07, indicate different collection locations and dates along the Napa River specific to the Napa River Flood Protection Project.

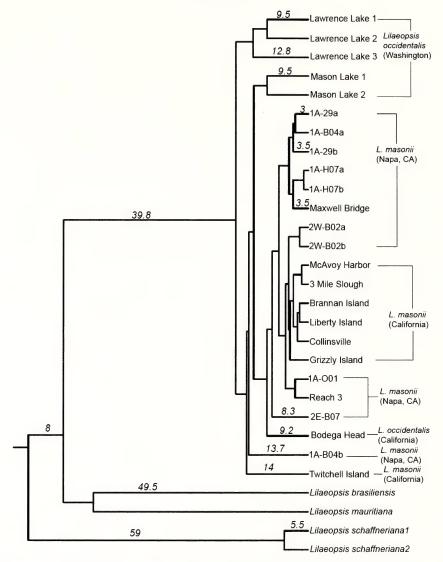


FIG. 4. UPGMA Cluster Phenogram (rooted and unrooted trees) from AFLP data matrix of five species of *Lilaeopsis*. Numbers are distance values. Codes for Napa collections, e.g., 1A-H07, indicate different collection locations and dates along the Napa River specific to the Napa River Flood Protection Project.

The morphological and geographic information to support two distinct taxa is weak, ambiguous, and unreliable at best.

Fallon's (2007) arguments regarding the importance of using genetic information to resolve taxonomic issues for species protection is borne out in our study. While her review focused solely on vertebrates, and on only those species, infraspecific or population segments proposed for listing, not those already listed, our results add further emphasis for use of molecular techniques in conservation efforts. We concur that multiple genetic markers are essential for a thorough assessment of taxonomic or population unit (or at any appropriate level) when considering of formal protection. We further suggest that

use of best available science such as existing or generating new genetic information is equally valid for the periodic reviews of listed species required of both the federal and state agencies. Further and relevant to *L. masonii*, use of genetic data is likely to be essential during a de-listing review process.

Based upon several lines of evidence, including decades of fieldwork throughout the range of *L. masonii*, observations from the most recent monograph (Affolter 1985), and our molecular genetic analyses, we urge that this rare taxon no longer be recognized as a separate taxonomic entity. Rather, *L. masonii* should be subsumed within the larger, much more widespread, common, and equally variable species, *L. occidentalis*.

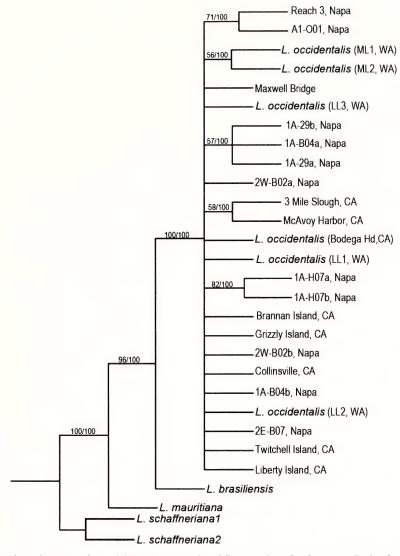


FIG. 5. Most parsimonious tree from AFLP data matrix of five species of *Lilaeopsis*. Codes for Napa collections, e.g., 1A-H07, indicate different collection locations and dates along the Napa River specific to the Napa River Flood Protection Project.

Significant morphological, but limited genetic, variation exists both within and among populations of *Lilaeopsis* throughout the Pacific Coast of North America, from the Queen Charlotte Islands in British Columbia to the inland islands of the Sacramento-San Joaquin Delta in the Great Valley of California. Importantly, this variation does not follow any consistent environmental gradient for either taxon. As such, one intrinsically variable species, not two, of west coast *Lilaeopsis* should be recognized in relevant floras, including those for North America.

Important additional circumstantial support comes from the very wide geographic ranges, some amphitropical, of the great majority of other species of *Lilaeopsis*, including *L. chinensis* Kuntze, *L. carolinensis*, *L. shaffneriana*, *L.* 

macloviana A. W. Hill, and L. novae-zelandiae, among others. A large geographic range is not surprising for all these species, given their vigorous vegetative reproduction by easily fragmented rhizomes and their restriction to aquatic habitats, many with bi- or multi-directional flow vectors (e.g., Napa River, Sacramento River, Pacific Ocean).

Field observations suggest a possible explanation for the inter- and intra-populational variation individual ramet size for both western North American *Lilaeopsis*. Periods of rapid spring growth occur during the spring tides and snowmelt from the Sierra Nevada, when temperatures warm sufficiently to encourage an increase in photosynthetic activity. This increased vegetative growth occurs when floodwaters from the

Sacramento, San Joaquin and Napa Rivers are at their height of volume and rate of flow. Thus, the comparatively high kinetic energy of flowing water during the spring run-off, coupled with this species' preference for river banks and shores characterized by high light and open exposure, combine to restrict vegetative growth to a comparatively shorter plant less vulnerable to being dislodged from its habitat. Relatively taller Lilaeopsis ramets are invariably found comparatively further from the shoreline in shadier and relatively lower energy microhabitats than comparatively shorter stature ramets. Aquaria enthusiasts who work with various species of Lilaeopsis have dubbed the short stature coupled with dense growth phenomenon the "lawn effect" (http:// www. freshwateraquariumplants.com).

Conversely, observations of *Lilaeopsis* species submerged in (low energy) water reveal individual leaves grow comparatively longer. Affolter's (1985) greenhouse experiments and observations that demonstrated that for least eight of the 13 species Lilaeopsis studied (including L. occidentalis), material grown in submerged pots had larger and wider leaves, more septae, and wider rhizome diameter. In his monograph of the thirteen species known in 1985, increased periods of inundation result in a suite of morphological changes, including an increase in leaf length and increases in both peduncle and pedicel lengths (Affolter 1985). Lastly, the rejection of leaf length as a key diagnostic character distinguishing two otherwise very similar taxa has precedent in Affolter's lumping of all Andean, Fuegian, and Patagonian material into a single species, L. macloviana, synonomizing thirteen previously described taxa.

Regulatory implications. Neither CESA nor the federal ESA, as amended, protects any vascular plant distinct population segment as does the ESA for specific vertebrate populations. While an argument can be made that this is a form of taxon chauvinism, plant species are not protected below the infraspecific level. Such a comparison is important, because some vertebrate species that were listed relatively soon after the ESA was passed have since been determined not genetically distinct from common widespread relatives, but they continue to be formally protected because of the DPS provisions. For example, the San Francisco garter snake (Thamnophis sirtalis tetrataenia), a highly restricted taxon in central coastal California, was determined, through an examination of the clade's mtDNA (Janzen et al. 2002), to be a member of a California clade of the widespread common garter snake. These authors concluded that morphologically based subspecies designations of T. sirtalis in western North America were invalid because they did not reflect reciprocal monophyly of mtDNA sequences.

Extrapolating Janzen et al.'s (2002) logic to our genetic work with *Lilaeopsis*, the parallel conclusion that the specific designation of *L. masonii* is invalid is compelling. Because neither the CESA nor the ESA include DPS provisions for plant species, *L. masonii* no longer warrants protection as a state "rare" species and the allocation of limited recovery resources. Given the widespread nature of *Lilaeopsis occidentalis* + *L. masonii*, and the large number of projects (both existing and proposed) requiring mitigation and monitoring of the rare *L. masonii*, a timely review of our findings is essential. Conservation dollars are few, and they should be applied to truly rare, threatened, and real discrete species.

Finally, Pavlik (2003) recently examined the role of state- and federally-listed species protecting the ecosystems in which they are found. Of relevance is the notion that some protected species provide a "regulatory umbrella" for other species that are unlisted, but are rare, in decline, or otherwise of conservation concern. Lilaeopsis masonii has long served to restrict, prevent, or slow the conversion, degradation or destruction of wetlands throughout the Sacramento-San Joaquin Delta, Suisun Marsh, and San Francisco Bay ecosystems, thereby protecting associated but unlisted species of conservation concern. While a suite of other protected wetland plant taxa exist in these ecosystems (e.g., Cirsium hydrophilum Jeps. var. hydrophilum [Suisun thistle], Cordylanthus mollis A. Gray ssp. mollis [soft bird's beak], etc.), there are many more that are rare, in decline, and not listed (e.g., Cicuta maculata Lam. var. bolanderi (S. Watson) G. A. Mulligan [Bolander's water hemlock], *Plantago* elongate Pursh [slender plantain], Lycopus asper Greene) (see Baye et al. 2000). Thus we acknowledge that a delisting of Mason's lilaeopsis may further expedite wetland habitat loss in central California. Nonetheless, conservation in the twenty-first century demands the use of best available science, despite the unintended consequences that may occur. Ultimately, government agencies charged with the protection of our biodiversity must redouble their efforts to embrace new scientific results that affect listed species, commit to diligent review of listed and candidate species, and disseminate accurate and up-to-date information. Similarly, conservationists should redouble their efforts to provide the best available science for decision-making. The time to embrace current molecular genetic techniques in routine conservation decision-making has come.

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### A COMPARISON OF THE EFFECTS OF NA<sub>2</sub>SO<sub>4</sub> AND NACL ON THE GROWTH OF HELIANTHUS PARADOXUS AND HELIANTHUS ANNUUS (ASTERACEAE)

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#### **ABSTRACT**

Helianthus paradoxus Heiser (Asteraceae, puzzle sunflower), is a federally threatened hybrid species found in salt marshes of west Texas and New Mexico. Helianthus annuus L. (Asteraceae, common sunflower) is one of the parent species and is found throughout North America, but it is not present in the inland salt marshes where H. paradoxus is found. Helianthus paradoxus has previously been described as a halophyte, but its tolerance to Na<sub>2</sub>SO<sub>4</sub>, one of the major salts found in its habitat, has not been investigated. However, salinity has been identified as a major abiotic factor influencing the limited distribution of H. paradoxus populations. In this greenhouse study, the effects of elevated concentrations of Na<sub>2</sub>SO<sub>4</sub> and NaCl, at equal ionic strengths (0.00, 0.09, 0.17, 0.34, and 0.51), on the survival and dry mass of both H. paradoxus and H. annuus were examined. In the three-way factorial experiment, the effects on dry mass observed were dependent on the species, the type of salt and the ionic strength of the salt. Helianthus paradoxus produced more dry mass than H. annuus in both salt treatments; however, NaCl was more inhibitory of dry mass production for both species with plants unable to survive the highest salt treatments. While dry mass of H. annuus decreased with increasing ionic strengths of both salts, dry mass of H. paradoxus increased by 38 to 72% in low to moderate ionic strengths of Na<sub>2</sub>SO<sub>4</sub> relative to the nonsaline treatment. Both species were less tolerant of NaCl than Na<sub>2</sub>SO<sub>4</sub> with *H. paradoxus* seeming to have moderate and high tolerance to elevated Cl<sup>-</sup> and SO<sub>4</sub><sup>2-</sup> ionic strength, respectively, while *H. annuus* had low to moderate tolerance. Greater dry mass production in Na<sub>2</sub>SO<sub>4</sub>, along with tolerance to both salts, suggests that low to moderate sulfate soil salinity will enhance the dry mass production of *H. paradoxus*.

Key Words: Halophyte, helianthus annuus, helianthus paradoxus, ionic strength, NaCl, Na<sub>2</sub>SO<sub>4</sub>, salt tolerance, sunflower.

Helianthus paradoxus Heiser (Asteraceae, puzzle sunflower) is a federally threatened species with limited distribution in salt marshes in west Texas and New Mexico (Correll and Johnston 1979; Poole and Diamond 1993; McDonald 1999). Hybridization studies (Heiser 1958, 1965; Abbott 1992) and molecular analysis (Rieseberg et al. 1990; Rieseberg 1991; Rieseberg et al. 1991) have determined that *H. paradoxus* is a stabilized hybrid species between H. annuus L. (Asteraceae, common sunflower) and H. petiolaris Nutt. (plains sunflower). Although *H. paradoxus* shares several morphological and ecophysiological traits with its parental species (Rosenthal et al. 2002), it has diverged and is genetically isolated from its progenitors and considered a separate species. Helianthus anuus is common throughout North America and grows in disturbed, heavy clay soils that are moist in the spring and dry out by midsummer. Helianthus petiolaris is found in dry, sandy soils in western North America, while H. paradoxus grows in heavy, waterlogged, saline soils (Van Auken and Bush 1998).

Ecological and ecophysiological studies of H. paradoxus have determined that this homoploid hybrid species is salt tolerant, unlike its parental species. Helianthus paradoxus is restricted to inland salt marshes with salt levels of approximately 10 g kg<sup>-1</sup> (Poole and Diamond 1993; U.S. Fish and Wildlife Service 2005; Grunstra and Van Auken 2007a, b), while *H. annuus* and *H.* petiolaris can be found in low saline soils (<0.02 g kg<sup>-1</sup> soil sodium, Welch and Rieseberg 2002). Helianthus paradoxus is a better competitor than its progenitors in saline soils (Bush and Van Auken 2004). The west Texas and New Mexico salt marshes were key habitats in isolating hybrids (Abbott 1992). The parental species are glycophytes and cannot survive the same habitat as *H. paradoxus*, where other salt tolerant plants are generally present (Poole and Diamond 1993; Lexer et al. 2003; U.S. Fish and Wildlife Service 2005). Additionally, H. paradoxus is capable of sequestering higher sodium and sulfur concentrations and produces greater leaf succulence compared to its parental species while maintaining significantly greater fitness when grown in elevated NaCl concentrations (Welch and Rieseberg 2002) or in field-like highly saline soil conditions (Karrenberg et al. 2006).

In the largest known population of *H. paradoxus*, at the Diamond-Y Spring Preserve near

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Fort Stockton, Texas, the distribution of H. paradoxus is mainly affected by soil salinity and soil moisture gradients when biotic factors are not considered (Bush and Van Auken 1997; Van Auken and Bush 1998; Bush 2006a, b). This large desert spring and associated salt marsh has had 1.44 to 2.70 million H. paradoxus plants (Van Auken and Bush 1998), depending on environmental conditions. In addition, there are several rare and federally endangered invertebrates found in the marsh (McDonald 1999). Helianthus paradoxus plants consistently establish parallel to the drainage of Leon Creek but their proximity depends on seasonal climatic conditions influencing soil salinity levels and soil water content, both of which decrease dramatically upland from the lowest point in the salt marsh (Van Auken and Bush 1998; Grunstra and Van Auken 2007a, b). When annual rainfall is high, H. paradoxus can be found further from the drainage compared to drier years when plants are located closer to the drainage. The population of *H. paradoxus* at the Diamond-Y Spring Preserve seems to be dependent on low to intermediate salinity levels and intermediate moisture levels; however, salinity appears to be the major abiotic factor affecting the local distribution of *H. paradoxus* (Bush 2006a, b).

Previous studies have identified H. paradoxus as a salt tolerant species with characteristics of halophytes (Welch and Rieseberg 2002; Bush and Van Auken 2004). However, these studies were done with NaCl, one of the major salt components of the marsh, but not Na<sub>2</sub>SO<sub>4</sub> which is also found at high concentrations in soils of its salt marsh habitat (Boghici 1997). In addition, the effects of a limited range of salinity levels have been examined. Chloride is generally more toxic than  $SO_4^{2-}$  and even Na<sup>+</sup> at lower concentrations (Manchanda et al. 1982; Marschner 1995; Franklin and Zwiazek 2004; Munns and Tester 2008); however,  $SO_4^{2-}$  salinity can be more growth inhibitive than Cl<sup>-</sup> for some halophytes (Warne et al. 1990; Egan and Ungar 1998). At the same time, separating specific ion effects is difficult and differential effects of  $Cl^-$  and  $SO_4^{2-}$  salinity on H. paradoxus are still unknown; consequently, the influence of these anions on the ecological isolation and distribution of H. paradoxus has not yet been elucidated.

Ionic strength rather than salt concentration was used as a treatment variable in the present study. It is used as a normalization procedure and was required because of different numbers of ions present in equal molar solutions of NaCl (2 ions) and Na<sub>2</sub>SO<sub>4</sub> (3 ions). Therefore, it was important to compare the two salts at concentrations that allowed osmotic potential of the corresponding treatments to be equal. Concentrations of the two salt treatments were based on equal ionic strengths calculated using procedures in Barrow (1966).

Table 1. Ionic Strengths of Each Treatment and Corresponding Salt Concentrations in  $G \cdot KG^{-1}$  Examined in the Study.

|                | NaCl | Na <sub>2</sub> SO <sub>4</sub> |
|----------------|------|---------------------------------|
| Ionic strength | (g   | $kg^{-1}$                       |
| 0.00           | 0    | 0                               |
| 0.09           | 5    | 4.1                             |
| 0.17           | 10   | 8.1                             |
| 0.34           | 20   | 16.2                            |
| 0.51           | 30   | 24.3                            |

The objective of this study was to examine the survival, growth and the salt tolerance of *H. paradoxus* in elevated levels of both Na<sub>2</sub>SO<sub>4</sub> and NaCl, at equal ionic strengths. Both of these salts are major contributors of the soil salts of the Diamond-Y Spring Preserve. Our experiment also included the more salt tolerant of its parental species, *H. annuus*, a known glycophyte.

### MATERIALS AND METHODS

Helianthus paradoxus seeds were collected from the Nature Conservancy's Diamond-Y Spring Preserve near Fort Stockton, Texas (31°00.54′N, 102°55.49′W) and stored dry at 25°C until used. Helianthus annuus seeds were purchased from Native American Seed Farm (Junction, Texas 76849) and stored dry at 4°C. Seeds of both species were cold stratified in Ziploc® storage bags lined with paper towels, wet with deionized water, and maintained at 4°C in the dark for 4 weeks (H. paradoxus) or 8 weeks (H. annuus). To prevent osmotic shock, groups of seeds (approximately 400 seeds for each treatment) were germinated on paper toweling saturated with deionized water (0.00 osmotic strength) in plastic storage bags at 25°C. Germinated seedlings were transferred to equal or increasing levels of the appropriate salt (NaCl and Na2SO4 at ionic strengths of 0.00, 0.05, 0.09, 0.13, 0.17, 0.26, 0.34, 0.43, and 0.51) every 2 d until placed in the final salt (NaCl or Na<sub>2</sub>SO<sub>4</sub>) and ionic strength to be tested (0.00, 0.09, 0.17, 0.34, and 0.51). Seedlings were kept in the appropriate solution for a total of 18 days prior to transplanting to pots in the greenhouse containing the corresponding treatment (Table 1).

For each species, five plants per pot with five replicate pots per treatment (25 plants per species per treatment) were grown for 62 d. Plastic pots (15 cm diameter × 15 cm height) lined with a Ziploc® storage bag (to retain water, salts, and nutrients) were filled with 1.4 kg of air-dried, sieved (5.8 mm mesh screen) soil. The soil was the upper 10 cm of a low nutrient Patrick-series Mollisol (clayey-over-sandy, carbonatic-thermic, typic calciustoll), collected from northern Bexar Co., Texas (Taylor et al. 1966; Van Auken and Bush 1998). The soil was friable, allowing root

Table 2. Three-Way ANOVA Results for the Total Dry Mass (G) of Two Species (*Helianthus Paradoxus* and *H. annuus*) Grown in Two Salts (NaCl and Na<sub>2</sub>SO<sub>4</sub>) and at Five Ionic Strengths (0.00, 0.09, 0.17, 0.34, and 0.51). All main effects and interactions were significant. <sup>a</sup> Significant interactions are designated (\* = P < 0.05; \*\* = P < 0.01; \*\*\* = P < 0.001; \*\*\*\* = P < 0.0001).

| Source <sup>a</sup>                      | df | SS    | F      | P        |
|--|----|-------|--------|----------|
| Species                                  | 1  | 4.11  | 35.69  | < 0.0001 |
| Salt                                     | 1  | 14.75 | 128.17 | < 0.0001 |
| Strength                                 | 4  | 5.00  | 43.44  | < 0.0001 |
| Species × salt***                        | 1  | 1.39  | 12.05  | 0.0008   |
| Species × strength**                     | 4  | 0.55  | 4.78   | 0.0016   |
| Salt × strength****                      | 4  | 1.67  | 14.50  | < 0.0001 |
| Species $\times$ salt $\times$ strength* | 4  | 0.40  | 3.51   | 0.0108   |
| Error                                    | 80 | 9.21  |        |          |
| Total                                    | 99 | 59.95 |        |          |

extraction and recovery (Bush and Van Auken 2004). Appropriate amounts of anhydrous salts (Na<sub>2</sub>SO<sub>4</sub> or NaCl) and a single nutrient application (0.05 g of P from  $Na_2HPO_4 \cdot 7H_2O$ , 0.07 g N from NH<sub>4</sub>NO<sub>3</sub>, 0.07 g of K from KCl, and 0.03 g of S from MgSO<sub>4</sub> · 7H<sub>2</sub>O; Tiedemann and Klemmedson 1986) were added to each pot and thoroughly mixed. Before seedlings were planted, 400 ml of deionized water was added to each pot. Thereafter, soil moisture was maintained at approximately field capacity with distilled water. This study was conducted in a fiberglass greenhouse in which the daytime temperatures ranged from approximately 26° to 38°C and light levels were approximately 36% of full sunlight with a mean photosynthetically active photon flux densities of  $562 \pm 135 \,\mu\text{mol m}^{-2} \,\text{s}^{-1}$  measured with a Li-Cor® Ll-188 integrating quantum sensor.

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Plant survivorship was assessed at 62 d for each treatment combination (species  $\times$  salt  $\times$  ionic strength). Percent survivorship is based on the mean number of erect and green plants out of five plants per replicate pot per treatment.

Shoot and root dry mass were measured at the end of the experiment. For shoot dry mass, plants from each pot were clipped at the soil surface and placed in a pre-weighed paper bag. For the ashfree root dry mass, all of the soil and particulate matter from each pot was carefully washed off the roots. Roots were then wrapped in preweighed aluminum foil. All plant material was dried in a forced air oven at 90°C to a constant mass. After drying, roots were ashed in a programmable muffle furnace (Fisher Scientific Isotemp®, Fisher Scientific Research, Pittsburgh, PA) at 625°C for 3 hours to obtain the ash-free root dry mass (Böhm 1979). Total dry mass was also calculated by combining the shoot dry mass and ash-free root dry mass per pot.

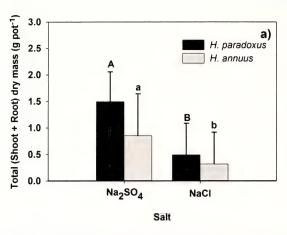
All dry mass data was analyzed using SAS statistical software (SAS Institute 1999) with each pot as the unit of replication and  $P \le 0.05$  as the criterion for significance. Any plant mortalities because of a treatment effect were taken into account by including a dry mass of zero. To

determine the effects of salt type and ionic strength on the dry mass of each species, a three-way ANOVA including interactions was employed. When significance was detected with the overall ANOVA, two-way and one-way ANOVAs were used followed by Duncan's Multiple Range Test to examine significant differences between all possible combinations of salt type and salt concentration for each species separately. Mean mortality was calculated, but was not analyzed statistically.

### RESULTS

All *H. paradoxus* and *H. annuus* plants died in the highest ionic strengths of NaCl examined (0.34 and 0.51). However, both species demonstrated 100% survivorship in the no-salt treatment. For all Na<sub>2</sub>SO<sub>4</sub> treatments, 100% of *H. paradoxus* plants survived, while 100% of the *H. annuus* plants survived in each of the Na<sub>2</sub>SO<sub>4</sub> treatments except at the 0.51 ionic strength, the highest Na<sub>2</sub>SO<sub>4</sub> concentration tested. Plant survivorship for *H. paradoxus* in NaCl treatments was 100% at the 0.09 and 0.17 ionic strengths, while 80% and 40% of *H. annuus* plants survived in these same ionic strengths, respectively.

Three three-way ANOVAs were used to analyze shoot, root, and total dry mass; however, only total dry mass data will be presented. Results were similar for mean shoot and root dry mass (analysis not shown). The three-way ANOVA (Table 2) demonstrated a significant overall species, salt, and ionic strength effect on total dry mass. In addition, the three two-way interactions were significant as was the three-way interaction. To demonstrate more clearly the experimental results, two of the two-way interactions will be presented first. Overall, H. paradoxus produced more dry mass than H. annuus in both salts (Fig. 1a, species  $\times$  salt interaction). For both species, more dry mass was produced in the Na<sub>2</sub>SO<sub>4</sub> treatment than in the NaCl treatment. In addition, ionic strength was significant with more dry mass in the lower treatments;



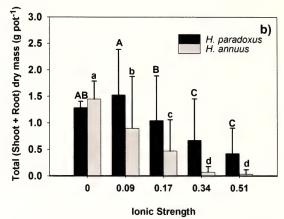


FIG. 1. Two-way interaction plots of total dry mass (bars) as the response variable for (a) salt (NaCl and Na<sub>2</sub>SO<sub>4</sub>) by species (*Helianthus paradoxus* and *Helianthus annuus*) and (b) ionic strength (0.00–0.51) by species. A three-way ANOVA determined there were significant differences (P < 0.0001) between salt treatments and ionic strengths for each species. Different letters indicate significant differences between means (Duncan's Multiple Range Test). Lines above the bars represent + one SD (standard deviation).

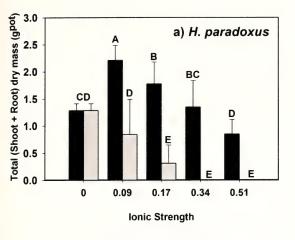
however, dry mass of *H. annuus* was significantly lower at an ionic strength of 0.09 (Fig. 1b, species  $\times$  ionic strength interaction). The salt  $\times$  ionic strength interaction has not been presented because the results can be seen within the three way interaction figure. The significant three-way interaction indicated that dry mass was dependent on species, salt type, and ionic strength (Table 2, Fig. 2a, b). Helianthus paradoxus dry mass was higher in Na<sub>2</sub>SO<sub>4</sub> compared to NaCl (Fig. 2a), with the greatest dry mass at the mid ionic strengths (Fig. 2a). On the other hand, H. annuus dry mass was lower than H. paradoxus, but H. annuus did produce more dry mass in Na<sub>2</sub>SO<sub>4</sub> compared to NaCl (Fig. 2b). In addition, as the ionic strength increased dry mass of H. annuus decreased.

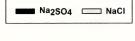
In comparison to the Na<sub>2</sub>SO<sub>4</sub> treatments, dry mass of both species was significantly reduced in NaCl at elevated ionic strengths (Duncan's Multiple Range Test, P < 0.0001, Fig. 2a, b). In the no-salt treatment, growth of *H. annuus* was elevated compared to H. paradoxus (not significantly). However, for all levels of salt addition, total dry mass of H. paradoxus was greater than H. annuus, yet the differences were salt dependent. For both species, mean total dry mass was elevated in Na<sub>2</sub>SO<sub>4</sub> at an ionic strength of 0.09 compared to NaCl. Dry mass of H. paradoxus was 32% greater than dry mass of H. annuus in this treatment. In the 0.17 to 0.51 ionic strengths of Na<sub>2</sub>SO<sub>4</sub>, mean total dry mass of *H. paradoxus* was 2- to 12-fold greater than H. annuus. Both species produced less dry mass in NaCl treatments; however, H. annuus dry mass was reduced most by NaCl. Total dry mass of H. paradoxus was 7-fold greater than *H. annuus* in the 0.09 NaCl treatment. This difference between species in NaCl increased at the 0.17 and 0.34 ionic strengths of NaCl where dry mass of *H. paradoxus* was 15-fold greater than *H. annuus*.

### DISCUSSION

Salt tolerance is the ability of a species to grow and adjust to the presence of a specific ion (ionic effect) or to adapt to the general effects of low water potentials (osmotic effect) (Ungar 1991). In this study, a potential ionic effect and an osmotic effect were investigated using NaCl and Na<sub>2</sub>SO<sub>4</sub> salts at increasing ionic strengths. Both salts are found in *H. paradoxus* habitats at various concentrations (Boghici 1997; Van Auken and Bush 1998; Lexer et al. 2003). To differentiate between the effects of the two salts and the Cland  $SO_4^{2-}$  anions, equal ionic strengths were used in the separate salt treatments (Barrow 1966). Due to greater salt tolerance of H. annuus in NaCl and mixed salt environments compared to H. petiolaris (both purported parental species) (Ashraf and Tufail 1995; Welch and Rieseberg 2002; Bush and Van Auken 2004; Karrenberg et al. 2006; DiCaterina et al. 2007), H. annuus was used as a comparative species for salt effects on growth of *H. paradoxus*.

As in previous studies, this investigation demonstrated that *H. paradoxus* was more salt tolerant than one of its parental species, *H. annuus*, and even produced slightly more dry mass in low saline soils compared to *H. annuus* (Figs. 1b, 2a, and 2b). *Helianthus paradoxus* produced 70% more dry mass than *H. annuus* over all treatments (data not shown) and consistently produced more dry mass in elevated salinity soils (Fig. 2a, b), especially in the sulfate treatments. Results of this greenhouse study are consistent with observations that *H. paradoxus* has greater fitness in saline conditions than *H.* 





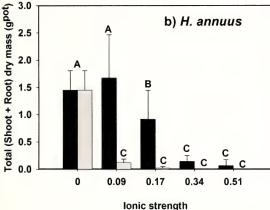


FIG. 2. Three-way interaction plots of total dry mass (bars) as the response variable for (a) *Helianthus paradoxus* and (b) *Helianthus annuus*. Salts were Na<sub>2</sub>SO<sub>4</sub> (black bar) and NaCl (gray bar) at ionic strengths of 0.00–0.51. A three-way ANOVA determined there were significant differences (P < 0.0001) between salt treatments and ionic strengths for each species. Different letters indicate significant differences between means (Duncan's Multiple Range Test) within a species. Lines above the bars represent + one SD (standard deviation).

annuus (Welch and Rieseberg 2002; Bush and Van Auken 2004; Karrenberg et al. 2006), and that *H. annuus* is not expected to be found in areas with elevated soil salinity where *H. paradoxus* is able to grow and outcompete *H. annuus* and probably other non-halophytic species (Abbot 2003; Van Auken and Bush 2006).

Both *Helianthus* spp. exhibited a specific ionic growth inhibition at elevated levels of Cl<sup>-</sup>, compared to SO<sub>4</sub><sup>2-</sup>, and differences in salt tolerance between species were evident. For both species, NaCl caused plant mortality at ionic strengths of 0.34 and 0.51, yet *H. paradoxus* was

more tolerant than H. annuus to low to moderate NaCl concentrations (Fig. 2). Greater dry mass production and survivorship of H. paradoxus plants compared to *H. annuus* in NaCl treatments was also observed by Welch and Rieseberg (2002) in corresponding NaCl treatments (100 and 200 mmol L<sup>-1</sup> [ $\sim$ 6 and 12 g kg<sup>-1</sup>] NaCl). Plant survivorship of *H. annuus* indicated that low Na<sub>2</sub>SO<sub>4</sub> levels seem to be less inhibitive than NaCl but significant dry mass reduction was still observed above 0.09 ionic strength treatments. Dry mass of *H. paradoxus*, on the other hand, was enhanced by low to moderate levels of Na<sub>2</sub>SO<sub>4</sub> with 38 to 72% greater dry mass, relative to the no-salt treatment. This corresponds to field observations where H. paradoxus was most abundant in soil salinities (mainly Na, K, Ca, and Mg chlorides with less SO<sub>4</sub>) ranging from 5 to 12 g kg<sup>-1</sup> in the Diamond-Y Spring Preserve (Boghici 1997; Van Auken and Bush 1998; Bush 2006b; Grunstra and Van Auken 2007a, b).

Although previous studies did not differentiate between the effects of NaCl and Na<sub>2</sub>SO<sub>4</sub> (Welch and Rieseberg 2002; Bush and Van Auken 2004; Karrenberg et al. 2006; Van Auken and Bush 2006), those studies support the salt tolerance of H. paradoxus to low concentrations of NaCl. Results consistently demonstrated that biomass of H. annuus was statistically reduced by NaCl alone (Welch and Rieseberg 2002) or by low levels of mixed salts (Na+, Cl-, and SO<sub>4</sub><sup>2-</sup> included; Bush and Van Auken 2004; Karrenberg et al. 2006), while H. paradoxus demonstrated lower productivity in NaCl alone and greater growth and productivity in the presence of  $SO_4^{2-}$ as observed in the present study. Greater salt tolerance of *H. paradoxus* to NaCl, as compared to *H. annuus*, has been attributed to significantly greater fitness along with Na<sup>+</sup> accumulation, leaf succulence, and water use efficiency (Welch and Rieseberg 2002). Because the salts were at equal ionic strengths and Na+ seems to serve as an osmoticum for *H. paradoxus* (Welch and Rieseberg 2002), it can be assumed that Cl<sup>-</sup> is causing reduced productivity in comparison to  $SO_4^{2-}$ . Molar concentrations of Cl<sup>-</sup> in the soil water of the Diamond-Y Spring Preserve are approximately 1.5 times that of molar concentrations of  $SO_4^{2-}$ ; therefore, Cl- has the potential of inhibiting growth of *H. paradoxus* in its salt marsh habitat (Boghici 1997). However, these data in conjunction with previous salt studies (Welch and Rieseberg 2002; Bush and Van Auken 2004; Karrenberg et al. 2006) indicate that the presence of soil sulfate may have played an important role in the selection for and adaptation of H. paradoxus to the Na-Cl<sup>-</sup>-SO<sub>4</sub><sup>2-</sup> rich environments. Further, poor tolerance to chloride and sulfate by *H. annuus* has limited its establishment and therefore, fitness in the H. paradoxus salt marsh habitat.

It should be noted that in order to maintain equal osmotic potentials between treatments, molar concentrations of Na<sup>+</sup> in NaCl treatments were 3.0 times that of Na<sub>2</sub>SO<sub>4</sub> treatments. Nevertheless, the molar equivalents of Na<sup>+</sup> at 0.09 and 0.17 ionic strengths were between that of the 0.34 and 0.51 ionic strengths of Na<sub>2</sub>SO<sub>4</sub> where dry mass production of *H. paradoxus* was not inhibited. Since an inert osmotic medium such as polyethylene glycol was not examined, an osmotic effect in combination with an ionic effect cannot be excluded (Katembe et al. 1998; Munns and Tester 2008).

In the limited studies comparing phytotoxicity of both salts, greater toxicity to NaCl compared to Na<sub>2</sub>SO<sub>4</sub> has been demonstrated for other salt tolerant glycophytes and halophytes (Manchanda et al. 1982; Curtin et al. 1993; Franklin and Zwiazek 2004; Pagter et al. 2009). Chloride is more toxic to plants than sulfate possibly due to synergistic phytotoxicity effects with Na<sup>+</sup>, differential inhibition of enzyme activity, reduction in plant productivity, and imbalance of nutritional status (Greenway and Munns 1980; Manchanda et al. 1982; Curtin et al. 1993; Wang et al. 1997; Veira Dos Santos and Caldeira 1999; Franklin and Zwiazek 2004). Ion toxicity is dependent on whether the plant possesses adaptations to tolerate the osmotic stress and to exclude and/ or compartmentalize the ion. Although not yet documented, it is possible that H. paradoxus accumulated Cl<sup>-</sup> along with Na<sup>+</sup> and may even be more sensitive to Cl<sup>-</sup> compared to SO<sub>4</sub><sup>2-</sup> due to poor compartmentalization into vacuoles (Greenway and Munns 1980; Flowers et al. 1986; Munns 1993; Rajakaruna et al. 2003). Chloride may be considered more toxic sometimes because of poor salt tolerance response and thus, high accumulation of Cl<sup>-</sup> over Na<sup>+</sup>, or in this case SO<sub>4</sub><sup>2-</sup>. Toxic cytoplasmic Cl<sup>-</sup> concentrations have not yet been determined but are assumed to be equal to or slightly lower than Na+ (Flowers et al. 1986; Greenway and Munns 1980; Munns and Tester 2008).

Sulfate may be required for salt tolerance in H. paradoxus. Tissue ion concentrations were not examined in this study, but previous work suggested that (as in other halophytes)  $SO_4^{2-}$ , along with Na+, may be an important vacuolar osmoticum in plant tissue (Greenway and Munns 1980; Karrenberg et al. 2006; Johnston 2006). Leaf sodium and sulfur concentrations were shown to be inversely related to calcium, magnesium, and potassium concentrations but positively related to biomass and succulence in H. paradoxus (Karrenberg et al. 2006). Interestingly, several studies have found a correlation between plants inhabiting waterlogged sulfate rich soils and the presence of vacuole stored flavonoid sulfates which may serve to detoxify excess sulfates alone or in combination with sodium

(Harborne 1975; Tomas-Barberan et al. 1987; Rajakaruna et al. 2003). A possible role of sulphur in the salt tolerance of halophytes also includes the production of methylated sulfonium compounds that accumulate in the cytosol as osmotically compatible organic solutes for compartmentalization of Na<sup>+</sup> and Cl<sup>-</sup> in vacuoles. These organic solutes also serve to detoxify sulfides in salt marsh plants (Flowers and Colmer 2008). Flavonoid sulfates or methylated sulfonium compounds have not been measured in tissues of *H. paradoxus*; however, Na<sub>2</sub>SO<sub>4</sub> tolerance of this species together with Na<sup>+</sup> and SO<sub>4</sub><sup>2-</sup> accumulation suggests a possible detoxification mechanism not yet identified.

Ecological isolation of *H. paradoxus* within the inland salt marshes of west Texas and New Mexico may in part depend on the elevated levels of soil salinity found in soils of these habitats (Boghici 1997; McDonald 1999; Van Auken and Bush 1998, 2006; Abbott 2003). Halophytes are limited to saline environments because of an advantageous adaptation to excess salts and a reduction of competitive ability in non-saline environments (Ungar 1991). Distribution of H. paradoxus plants appears to be dependent on low to moderate soil salinity levels at the Diamond-Y Spring Preserve where Na<sup>+</sup>, Cl<sup>-</sup> and SO<sub>4</sub><sup>2-</sup> are the prevalent salts from groundwater discharge, while Ca<sup>2+</sup>, Mg<sup>2+</sup>, and HCO<sub>3</sub><sup>-</sup> are secondary ions (Boghici 1997; Van Auken and Bush 1998; Bush 2006b; Grunstra and Van Auken 2007a, b). In the present study, H. paradoxus outperformed H. annuus in both soil salt treatments, partially explaining the inability of H. annuus to survive the salt marsh habitat of H. paradoxus (Lexer et al. 2003; Bush and Van Auken 2004). The presence of salts excluded H. annuus from colonizing the salt marsh (Abbott 2003; Lexer et al. 2003), while the salt tolerance of H. paradoxus to both NaCl and Na<sub>2</sub>SO<sub>4</sub> has allowed this species to establish in the Diamond-Y Spring Preserve and other salt marsh environments in west Texas and New Mexico. Further, tolerance to high concentrations of Na<sub>2</sub>SO<sub>4</sub>, as demonstrated by significantly greater productivity relative to non-saline conditions, suggests that H. paradoxus may experience a physiological stress response without elevated Na<sub>2</sub>SO<sub>4</sub>, which is necessary for optimum growth and perhaps necessary for salt tolerance (Munns and Tester 2008). The establishment of *H. paradoxus* in the Diamond-Y Spring Preserve has been promoted by the selection for transgressive phenotypes promoting salt tolerance (sodium exclusion, calcium uptake, and leaf succulence), as demonstrated by *H. paradoxus*, along with the presence of specific ions (Na<sup>+</sup>, Ca<sup>2+</sup>, and SO<sub>4</sub><sup>2-</sup>) in the salt marsh habitat (Abbott 2003; Lexer et al. 2003; Karrenberg et al. 2006). In addition, both parental species are poor competitors in field-like

elevated soil salinity conditions, while *H. paradoxus* is a poor competitor against *H. annuus* in nonsaline conditions (Bush and Van Auken 2004).

The potential for hybridization is still present and environmental conditions isolating hybrid Helianthus spp. from parental genotypes appears to have been an important factor in their adaptive evolution of greater fitness in their respective habitats (Lexer et al. 2003; Whitney et al. 2010; Donovan et al. 2010). Populations of H. annuus are found in disturbed pockets of isolated deep, nonsaline soil. Helianthus petiolaris, the other reported parent species to H. paradoxus is also found in some isolated, low saline, sandy soils. However, environmental factors such as the soil conditions required for the isolation and survival of some of the H. annuus  $\times$  H. petiolaris hybrids was and continues to be the saline soils surrounding the isolated springs in this area of west Texas and New Mexico (Abbott 2003; Lexer et al. 2003). The unique salt tolerance of H. paradoxus compared to its parental species along with establishment in the Na+-Cl--SO<sub>4</sub>2- dominated salt marshes will continue to promote the ecological isolation of *H. paradoxus*.

### ACKNOWLEDGMENTS

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### THE DIVERSITY AND BIOGEOGRAPHY OF THE ALPINE FLORA OF THE SIERRA NEVADA, CALIFORNIA

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#### ABSTRACT

The alpine zone of the Sierra Nevada of California, defined as non-forested areas at or above 3500 m, includes 385 species (409 taxa) of native vascular plants. Were the alpine boundary defined as at or above 3300 m, the alpine flora would grow to 536 species (570 taxa). There are 97 species that reach elevations of 4000 m and 27 species that reach to 4200 m. Over half of the alpine species occur in just six families, led by the Asteraceae (55 species, 59 taxa), Poaceae (39 species, 47 taxa), Brassicaceae (34 species), and Cyperaceae (31 species). The largest genus present is Carex with 29 species, and 18 more species would be added by lowering the alpine boundary to 3300 m. Next in size are Draba (14 species) and Lupinus (11 species, 16 taxa). Life forms of the flora are heavily dominated by broadleaved erect perennials (50%), followed in importance by graminoid perennials (21%) and mats and cushions (11%). Annuals and woody shrubs each account for about 6% of the flora. Only nine species are obligate alpine taxa with a range restricted to elevations of 3500 m or above. An additional 67 species (17% of the flora) occur in both subalpine and alpine habitats but not lower. More than a quarter of the alpine species have elevational ranges that extend as low as foothill habitats defined as occurring below 1200 m. In terms of biogeographic affinities, the broad relationships of the flora include the cordillera of western North America (35%), Intermountain region of the Great Basin (20%), Sierra/Cascade axis (16%), and widespread distributions (14%). There are 36 species in the alpine flora endemic to the Sierra Nevada, and another 31 species that are Californian endemics.

Key Words: Alpine, arctic-alpine flora, cushion plant, Sierra Nevada, treeline.

How large and diverse is the alpine flora of the Sierra Nevada in California and what are its biogeographic relationships? There has been a long history of floristic and ecological studies of the alpine region of the Sierra Nevada addressing this and related issues, but a clear answer to the question has not been achieved. Unlike the majority of alpine regions in the northern hemisphere that share extensive elements of a circumboreal arctic-alpine flora, the Sierra Nevada has developed a unique component to its alpine flora under the influence of mediterraneanclimate conditions with relatively dry summers added to other alpine environmental factors of stress. Also significant in the evolution of this alpine flora has been the relative isolation of the range from other high mountain floras of the western United States. Moreover, the Sierra Nevada possesses a complex mosaic of substrate, glacial history, and soil variation superimposed over broad patterns of climatic and topographic heterogeneity.

Interest in the alpine flora dates back to early descriptions by Coville (1893) and Harshberger (1911), who recognized the distinctiveness of the Sierran alpine flora. Hall and Grinnell (1919) gave a very brief description of the alpine zone in the context of a broader description of California life zones, and provided a short list of characteristic species. More significant, however, have

been five studies over the past 80 years that have provided an analysis of the diversity and floristic affinities of the high elevation flora of the Sierra Nevada. The earliest of these was the work of Smiley (1921), whose definition of the boreal region of the Sierra Nevada comprised the Canadian, Hudsonian, and Arctic-Alpine zones as characterized in the Merriam system of life zones (Daubenmire 1938). These life zones roughly correspond to the upper montane, subalpine and alpine zones under current concepts (Fites-Kaufman et al. 2007). Smiley's work was followed by the classic investigation of Sharsmith (1940), and in more recent decades with analyses by Chabot and Billings (1972), Major and Taylor (1977), and Stebbins (1982). Early speculations on the origin of the Sierran alpine flora were contributed by Went (1948, 1953). Beyond these broad floristic surveys, there have been numerous studies of the floristics and vegetation of regional areas of subalpine and alpine vegetation in the Sierra Nevada (Howell 1944, 1951; Klikoff 1965; Pemble 1970; Taylor 1976b; Major and Taylor 1977; Tatum 1979; Benedict and Major 1982; Burke 1982; Ratliff 1982; Benedict 1983; Porter 1983; Constantine-Shull 2000; Sawyer and Keeler-Wolf 2007).

None of the existing literature has provided a satisfactory answer to the fundamental question. How many species are there in the alpine flora of

the Sierra Nevada? The objective of this paper is to present a broad overview of the alpine flora of the Sierra Nevada by providing a detailed and updated analysis of the floristic richness, ecological diversity, and biogeographic relationships of the species present within the alpine zone. The paper takes a conservative approach following Sharsmith (1940) by defining the alpine zone using a lower elevational limit of 3500 m. Climatic treeline typically occurs from 3300– 3500 m in the central and southern Sierra Nevada where the great majority of alpine habitat in California is located (Fig. 1). Although the northern Sierra Nevada lacks high elevation areas, it nevertheless has a good representation of alpine species that reach above 3500 m in the central or southern areas of the range. To provide a broader context examining the significance of elevation in the definition of the alpine zone, analyses have been made for all species occurring at or above 3300 m within California.

Beyond an intrinsic interest in the evolution of biodiversity of alpine biota, there are very significant reasons to support Sierran alpine studies that can serve as baseline studies for important early warning systems of potential environmental impacts of climate change. Climate change models for California suggest that there will be significant effects on environmental conditions of subalpine and alpine habitats of the Sierra Nevada (Hayoe et al. 2004; Shafer et al. 2001), and historical data on vertebrate distribution demonstrates that these effects are ongoing today in influencing the distributions of vertebrate species (Moritz et al. 2008; Tingley et al. 2009).

### MATERIALS AND METHODS

The Jepson Manual, 2nd Edition (Baldwin et al. 2012) was used to identify California species with an elevational distribution up to or above 3300 m within the state, and which occurred in the Sierra Nevada. This reference is the sole source and reference for binomials used in this article. Species at or above 3500 m in California were considered to comprise the alpine flora. The upper and lower elevational ranges of each of these species were recorded, along with their biogeographic distribution and occurrence within the geographic regions of California (Hickman 1993). These geographic regions included records of species presence in the montane and higher elevations of the northern, central, and southern subregions of the Sierra Nevada, as well as the high Cascade Range, the Klamath/Siskiyou mountains, Transverse and Peninsular ranges of southern California, and ranges east of the Sierra Nevada including the Sweetwater and White-Inyo mountains (Fig. 1). The elevational limits and geographical ranges listed in Baldwin et al.

(2012) are specimen-based records and thus considered reliable. Only native species were included in this analysis, however, alien species recorded as occurring at high elevations in the Sierra Nevada are very few. *Poa pratensis* L. is recorded as reaching 3500 m and *Taraxacum officinale* F. H. Wigg, reaches 3300 m.

Each taxon occurring at elevations of 3300 m or above was categorized into a series of growth forms, based on a modified scheme of Raunkiaer (1934). These categories were broad-leaved herbaceous perennials (tussocks, rosettes, and biennials), graminoid perennials, mats and cushion plants, geophytes, aquatics, annuals, subshrubs, woody shrubs (deciduous and evergreen), and trees.

The lower elevational limit of occurrence in California was used to separate alpine species into categories of lowest elevational zone of occurrence on the following basis: 1) foothill habitats of woodland and chaparral— <1199 m; 2) lower montane habitats dominated by mixed conifer and yellow pine forests— 1200–1999 m; 3) upper montane habitats of red fir and lodgepole pine forests— 2000–2699 m; 4) subalpine habitats of open conifer stands near treeline— 2700–3499 m; and 5) alpine habitats— >3500 m. Because elevational boundaries of these major vegetation zones change with latitude, as well as locally with slope exposure, these elevational ranges represent averaged boundaries across the west slope of the central and southern Sierra Nevada.

The biogeographic range of each alpine species was classified into one of six categories. These were: 1) widespread species present in many habitats or regions across North America and/or throughout the world; 2) cordilleran species broadly distributed in mountain regions of the western United States; 3) Sierra/Cascade species with a Pacific Northwest distribution; 4) Intermountain Region species present in the Great Basin; 5) species endemic to the Sierra Nevada; and 6) species endemic to California, broadly defined to include adjacent Great Basin ranges extending into western Nevada (i.e., Sweetwater, Wassuk, and White-Inyo mountains) and southern Oregon. Dividing species into such simple biogeographic categories is inherently arbitrary for some species, and expanded field studies in the future may well change these classifications and alter the list of Sierran endemics based on new records or taxonomic revisions.

### RESULTS

The Geography of California Alpine Habitats

The elevational contour interval of 3500 m is highly irregular in the Sierra Nevada, as it defines a relatively continuous area along the crest of the

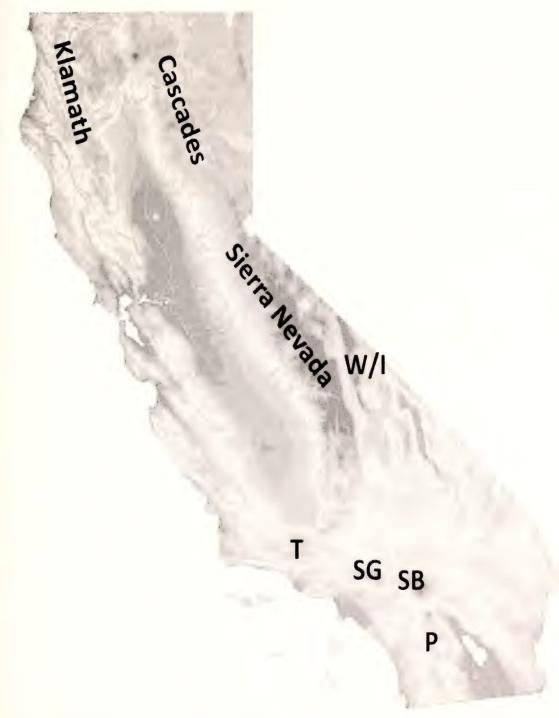


FIG. 1. Topographic map of California showing the major areas of mountain systems. W/I = White-Inyo Mountains, T = Tehachapi Mountains, SG = San Gabriel Mountains, SB = San Bernardino Mountains, and P = Peninsular Ranges.

central and southern crest of the range extending from northern Tuolumne and Mono counties in the area of Leavitt Peak (3527 m) near Sonoran Pass and south across Yosemite National Park where the highest peak is Mount Lyell (3999 m;

Fig. 2). Further south this belt of alpine habitat continues into Kings Canyon and Sequoia National parks where there are extensive areas of alpine habitat with ten peaks that reach above 4000 m. Mount Whitney at 4421 m is the highest

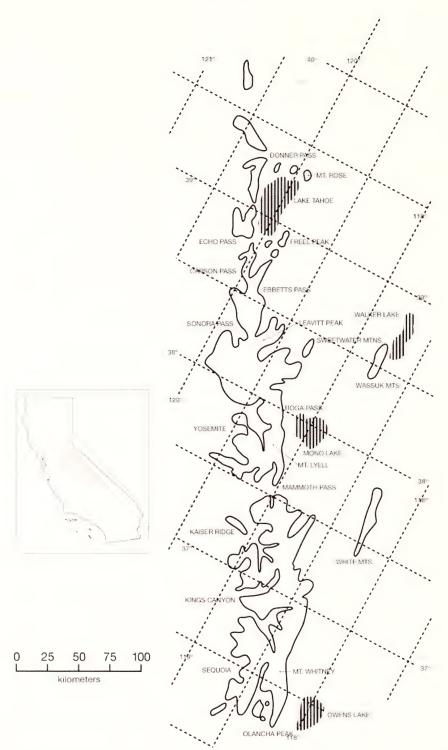


Fig. 2. Geographic distribution of high elevations of the Sierra Nevada and adjacent ranges. The solid line marks a rough position of the 3000 m contour. Adapted from Hovanitz (1940).

point in the contiguous United States. The southern limit of this extensive and virtually contiguous alpine zone occurs at Cirque Peak (3932 m) in Sequoia National Park at the southern

end of the continuous chain of glaciated peaks in the Sierra Nevada. To the south, the alpine zone reappears on Olancha Peak (3698 m; Fig. 2), the southernmost glaciated summit of the range lying on the Tulare-Inyo county line (Howell 1951; Tatum 1979). Two major breaks with subalpine elevations but not true alpine provide the only major discontinuity for this primary Sierran alpine region. These are Tioga Pass in Yosemite National Park (3031 m) and Mammoth Pass (Minaret Summit) (2824 m), which is the route for California Highway 203.

The crest of the Sierra Nevada lies at lower elevations to the north of the Tioga Pass area, with only scattered areas of good alpine habitat present. A notable ecological change occurs north of this pass where volcanic substrates replace the granites of the central and southern Sierra Nevada. Fragmented communities of alpine species are present at elevations below 3500 m, particularly along exposed ridgelines and on steep north-facing slopes that were heavily glaciated. However, there are no elevations in the northern Sierra Nevada that reach the 3500 m limit used here to define the alpine zone. Alpine habitats are weakly developed in Alpine Co. (with Sonora Peak reaching 3493 m) and eastern El Dorado Co. (with Freel Peak reaching 3318 m), extending to their northern limit on Mount Rose (3285 m) in the Carson Range east of Lake Tahoe in Nevada (Fig. 2). Nevertheless, there are scattered communities of alpine-like habitat existing at upper elevations in the northern Sierra Nevada, positioned above local edaphically-controlled treelines, and the alpine flora is well represented (Smiley 1915). Despite the floristic relationships of high elevation Sierran species all along the range, Stebbins and Major (1965) linked the Sierra Nevada north of Lake Tahoe with the Cascade Range rather than with the region of the central and southern Sierra Nevada on the basis of the dominance of volcanic substrates.

To the north of the Sierra Nevada, Mount Shasta in the southern Cascade Range reaches an elevation of 4322 m, while Lassen Peak is lower at 3187 m. The highest peaks in the Klamath Mountains of northwestern California and adjacent Oregon are Mount Eddy (2750 m) in Siskiyou Co., Thompson Peak (2744 m) in Trinity Co., and Mount Ashland (2296 m) in Jackson Co., Oregon. These high peaks contain areas with permanent or long-lasting snowfields on north-facing slopes with associated alpine species (Howell 1944; Major and Taylor 1977).

There are several high mountain ranges to the east of the Sierra Nevada at the western margin of the Great Basin. The Sweetwater Mountains, located just 33 km east of the Sierra Nevada, reach 3552 m on Mount Patterson (Hunter and Johnson 1983). The Wassuk Range in west-central Nevada lie 48 km east of the Sweetwater Mountains and 88 km north of the White Mountains, reaching 3427 m on Mount Grant (Bell and Johnson 1980). The White Mountains

have an extensive alpine area and reach to 4344 m on White Mountain Peak, the third highest peak in California (Rundel et al. 2008). To the south, Mount Waucoba forms the high point at 3390 in the Inyo Mountains. The Panamint Mountains lying east of the White-Inyo Mountains reach a maximum elevation of 3366 m on Telescope Peak. Further south, the Spring Mountains in southwestern Nevada divide the Pahrump Valley and Amargosa River basins from the Las Vegas Valley watershed and define part of the southwestern boundary of the Great Basin. The highest point is Charleston Peak at 3633 m.

High elevations are also present in the Transverse and Peninsular ranges of southern California (Fig. 1) where a subset of Sierran alpine species is present in weakly developed alpine-like communities (Hall 1902; Parish 1917; Horton 1960; Hanes 1976; Major and Taylor 1977; Meyers 1978). Mount San Gorgonio in the San Bernardino Mountains reaches 3506 m, while other high points are Mount San Jacinto in the San Jacinto Mountains at 3302 m and Mount Baldy in the San Gabriel Mountains at 3068 m. Alpine species are present in both xeric and mesic habitats at high elevation, but alpine communities, defined as extended areas dominated by assemblages of alpine species, are only poorly developed.

The alpine zone of the Sierra Nevada experiences mediterranean-type climate conditions that differ significantly from those that characterize the Rocky Mountains and most of the continental alpine habitats of the world where summer rainfall predominates. The fraction of annual precipitation that falls as winter snow in the Sierra Nevada is about 95% at upper treeline (Stephenson 1998). Deep snow packs and cool temperature at higher elevations mean that snowmelt extends into the spring, but the length and magnitude of the summer drought period experienced by plants is significant. Patterns of rainfall decline gradually from north to south in the Sierra Nevada, and summer drought decreases as elevation increases because of both increased levels of precipitation and cooler temperatures with lower evaporative demand at higher elevations (Stephenson 1998; Urban et al. 2000).

Winter mean monthly low temperatures are moderate in the Sierra Nevada compared to the Rocky Mountains, and soils only rarely freeze to even moderate depth. While, the mean minimum temperature above treeline is below freezing for ten months of the year, with nighttime lows that typically reach only -3 to  $-6^{\circ}$ C, although extremes can reach temperatures of  $-15^{\circ}$ C or lower on the high peaks. Nevertheless, these moderate low temperatures as well as other limiting factors for survival at high elevations sharply reduce the diversity of species able to tolerate such conditions (Körner 2003).

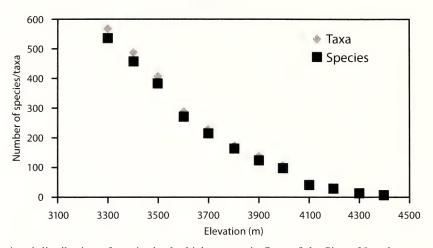


FIG. 3. Elevational distribution of species in the high mountain flora of the Sierra Nevada.

### Floristic Richness

The alpine flora of the Sierra Nevada, defined as species reaching 3500 m or more at their upper limit of distribution, comprises 385 vascular plant species. The species total includes 10 ferns and fern relatives (2.6%), five conifers (1.3%), 85 monocots (22.1%), and 285 eudicots (74.0%). With the inclusion of an additional 24 named varieties and subspecies, the total number of alpine taxa is 409.

Of course, the predetermined elevational boundary has a very strong influence on the size of the flora (Fig. 3). If the alpine flora were defined as those species reaching to 3400 m, then 76 additional species would be added for a total of 460 species (488 taxa). Were the limit defined as 3300 m, there would be a flora of 536 species (570 taxa), with the relative proportions of monocots and eudicots virtually unchanged and the addition of five ferns and one conifer.

There are 97 species (101 taxa) with an elevational range that extends as high as 4000 m, an elevation reached by only the highest Sierran peaks (Fig. 3). This number declines to 27 species that reach 4200 m in elevation. These 27 high elevation species do not display dominance by a few families as is the case with the full alpine flora but are rather spread among 15 different families (Appendix 1). Three species have been recorded as reaching to 4400 m. These are Epilobium anagallidifolium Lam. (Onagraceae), Saxifraga hyperborea R. Br. (Saxifragaceae), and Erigeron vagus Payson (Asteraceae). Additional taxa that occur up to or above 4300 m are Erigeron compositus Pursh (Asteraceae), Boechera lemmonii (S. Watson) W. A. Weber (Brassicaceae), Cerastium beeringianum Cham. & Schltdl. (Caryophyllaceae), Calyptridium umbellatum (Torr.) Greene (Montiaceae), Festuca brachyphylla Schult. & Schult. subsp. breviculmis Fred., Poa keckii Soreng. and P. lettermannii Vasey (Poaceae), *Phlox pulvinata* (Wherry) Cronquist (Polemoniaceae), *Ranunculus eschscholtzii* Schltdl. var. *oxynotus* (A. Gray) Jeps. (Ranunculaceae), and *Potentilla pseudosericea* Rydb. and *Sorbus californica* Greene (Rosaceae).

There are six families that contribute 20 or more taxa to the alpine flora. The largest of these is the Asteraceae with 55 species (59 taxa), followed in size by the Poaceae (39 species, 47 taxa), Brassicaceae (34 species), Cyperaceae (31 species), Rosaceae (21 species, 23 taxa), and Fabaceae (18 species, 27 taxa). These six families together comprise 52% of the alpine flora.

At the generic level, *Carex* stands out prominently with 29 species in the alpine flora, with an additional 18 species present at elevations between 3300 and 3500 m. Next in order of size are *Draba* (Brassicaceae, 14 species), and *Lupinus* (Fabaceae, 11 species, 16 taxa). There are 10 species of *Boechera* (Brassicaceae) and nine species each of *Epilobium* (Onagraceae), *Eriogonum* (Polygonaceae), and *Potentilla* (Rosaceae). There are three genera with eight species—*Penstemon* (Plantaginaceae), *Poa* (Poaceae), and *Salix* (Salicaceae).

### Growth Form Distribution

Herbaceous perennial growth forms, broadly defined, comprise the great majority of taxa reaching to or above 3500 m in the Sierra Nevada. This growth form with all of its subgroups includes 343 taxa, or 84% of the 409 taxa that comprise the flora. These herbaceous perennials can be broken down into subgroups of erect herbaceous perennials, perennial graminoids, prostrate mats and cushion plants, biennials, and geophytes. The largest numbers of herbaceous perennials form the category of erect herbaceous perennials, with 186 species (206 taxa; Fig. 4). The most important families for the erect herbaceous perennials are the Asteraceae, Brassi-

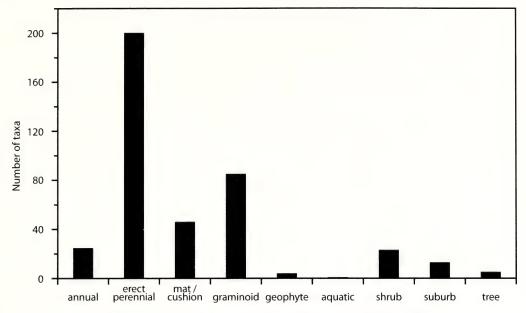


FIG. 4. Growth form distribution of alpine taxa in the alpine flora of the Sierra Nevada.

caceae, Fabaceae, Rosaceae, Polygonaceae, and Onagraceae. Among the erect herbaceous perennials are four species that are reported to have the potential to survive as facultative annuals. Although these have not been studies in detail, it is expected that these species have biennial or short-lived perennial life histories in the alpine zone, and they are included here in the totals for erect herbaceous perennials. Three of these are members of the Brassicaceae, each representing a different genus. Among these facultative annuals, only *Androsace septentrionalis* L. (Primulaceae) with an elevation range of 2700–3600 m can be considered as a subalpine and alpine specialist.

There are several additional groups classified broadly as erect herbaceous perennials. The 10 species of ferns and fern relatives included here within the alpine flora represent four families (Pteridaceae, Ophioglossaceae, Woodsiaceae, and Selaginellaceae). Four of these species reach elevation at or above 4000 m—Botrychium lineare W. H. Wagner, B. paradoxum W. H. Wagner, Cystopteris fragilis (L.) Bernh., and Selaginella watsonii Underw. Lowering the characterization of the alpine zone lower limit to 3300 m would add five additional fern species (Appendix 2). Also classified as erect perennials are seven species of hemiparasites, all members of the Orobanchaceae, with four species (five taxa) of Castilleja and three species of Pedicularis. Six more species from this family would be added by lowering the alpine boundary to 3300 m, including five more species of Castilleja.

Next in diversity among the herbaceous perennials is the subgroup of graminoids (Cyperaceae, Juncaceae, Juncaginaceae, and Poaceae) with 83 species (85 taxa, Fig. 4). All of the members of these four families within the alpine flora are perennials, with *Agrostis, Bromus, Carex, Elymus, Juncus, Luzula, Poa,* and *Stipa* forming genera with five or more taxa (Appendix 1). These perennial graminoids include one species of C<sub>4</sub> grass, *Muhlenbergia richardsonis* Rydb. (Sage and Sage 2002). Two other C<sub>4</sub> members of this genus, the perennial *M. montana* Hitchc. and the annual *M. filiformis* Rydb., just miss inclusion, reaching to elevations of 3420 m and 3350 m, respectively. Lowering the alpine boundary to 3300 m would add significantly to the diversity of graminoid perennials, with 43 additional taxa present (Appendix 2).

Prostrate mats and cushion forms of growth are common in some of the herbaceous perennials of the Sierran alpine flora (Fig. 4). These species are low in stature and form a heterogeneous group that shares the characteristic of a prostrate growth form with either a central taproot or multiple points of rooting through layering. Mats and cushions often form an ecologically significant component of plant cover on exposed ridges and fellfield. There are 46 species classified here as mats or cushions, with 19 of these high subalpine and alpine specialists not occurring below 2700 m elevation The growth form characteristics of mats and cushions may be genetic in some cases but in others is environmentally induced, with mat forms of growth only occurring at higher elevations (personal observations). Alpine mat and cushion species are well represented in the Asteraceae with 13 species (notably taxa of Antennaria and Erigeron), Polygonaceae (*Eriogonum*) with eight species,

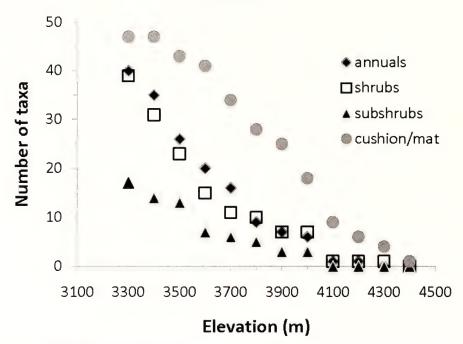


Fig. 5. Elevational distribution of taxa of annuals, shrubs, subshrubs, and mats/cushions in the alpine flora of the Sierra Nevada.

Brassicaceae (*Draba* and *Anelsonia*) with six species, and Fabaceae (*Astragalus*, *Lupinus*, *Oxytropis*, and *Trifolium*) with five species. Also notable in their ecological dominance are mats of Caryophyllaceae (*Cerastium*, *Eremogone*, *Minuartia*) and Polemoniaceae (*Phlox*).

The alpine flora includes just four species of geophytes, which represent the Alliaceae (Allium obtusum Lemmon var. obtusum), Liliaceae (Calochortus leichtlinii Hook. f.), Melanthiaceae (Veratrum californicum Durand var. californicum), and Themidaceae (Triteleia dudleyi Hoover). The highest elevation species among these is C. leichtlinii, which reaches up to 4000 m. None of these geophytes can be considered to be high elevation specialists as all reach lower elevational limits of 1200-1500 m in California. There are six species of geophytes that just miss reaching the lower alpine limit, as defined here, but occur at or above 3300 m (Appendix 2). These include *Allium* validum S. Watson (Alliaceae), Iris missouriensis Nutt. (Iridaceae), Lilium kelleyanum Lemmon (Liliaceae) and three Orchidaceae (Platanthera dilatata (Pursh) Lindl. ex L. C. Beck var. leucostachys (Lind.) Luer, P. sparsiflora Schltr., and Spiranthes romanzoffiana Cham.

Only a single species of aquatic plant, *Callitriche palustris* L. (Plantaginaceae), reaches the alpine zone of the Sierra Nevada. This is perhaps not surprising given the relatively small area of oligotrophic lakes that are present above 3500 m. *Potamogeton robbinsii* Oakes (Potamogetonaceae) and *Limosella acaulis* Sessé & Moc.

(Scrophulariaceaeae) have a range that extends as high as 3300 m, and a number of aquatic species including *Isoetes* (Isoetaceae) reach elevations of 3000 m.

Plants with an annual life history comprise a small but significant component of the alpine flora of the Sierra Nevada, with 24 species (26 taxa) reaching to elevations of 3500 m (Fig. 4). The annual species occurring at the highest elevation is Gayophytum decipiens F. H. Lewis & Szweyk. (Onagraceae), which ranges up to 4200 m. Five other species of annuals reach 4000 m in elevation—Gentianopsis holopetala (A. Gray) Iltis (Gentianaceae), Phacelia hastata Douglas ex Lehm. subsp. compacta (Brand) Heckard (Boraginaceae), Mimulus suksdorfii A. Gray (Phrymaceae), Gayophytum racemosum Torr. & A. Gray (Onagraceae), and Collinsia torreyi A. Gray var. wrightii (S. Watson) I. M. Johnst. (Plantaginaceae). The number of annual species present increases sharply below the limit set here for inclusion in the alpine flora. Including the above taxa, there are 33 annual species (36 taxa) with a range reaching to or above 3400 m and 38 species (41 taxa) occurring at or above 3300 m (Fig. 5).

Most of the annuals reaching into the alpine zone are species with wide elevational ranges that extend down to lower foothill habitats. Only 13 of the alpine annual species have ranges limited to elevations at or above 1200 m, a distribution that would indicate adaptation to montane and higher elevation habitats. Five annual taxa can be

considered as subalpine and alpine specialists having a lower elevation limit of 2700 m or above and/or a median elevational range above 3000 m. These species, none of which ranges as high as 4000 m or above, are Comastoma tenellum (Rottb.) Toyok. (Gentianaceae), Cryptantha circumscissa (Hook. & Arn.) I. M. Johnst.var. rosulata J. T. Howell (Boraginaceae), Streptanthus gracilis Eastw. (Brassicaceae), and Leptosiphon oblanceolatus (Brand) J. M. Porter & L. A. Johnson and Gymnosteris parvula A. Heller (Polemoniaceae). Just missing this criteria, but certainly also a high elevation specialist, is Phacelia orogenes Brand (Boraginaceae). Four of these six, with Comastoma tenellum and Gymnosteris parvula as exceptions, are Sierra Nevada endemics.

The most important family in contributing to the annual flora of high elevations is the Boraginaceae, with 11 species (12 taxa) representing five genera. Next in importance are the Polemoniaceae with five species (comprising five genera), and the Onagraceae with four species (five taxa) representing just a single genus. There are four genera that contribute three or more species to the annual flora. These are Gayophytum (Onagraceae, four species, five taxa), Phacelia (Boraginaceae, four species), Cryptantha (Boraginaceae, three species, four taxa), and Mimulus (Phrymaceae, three species).

Subshrubs, defined as semi-woody species that maintain living perennial tissue in winter above the ground surface, include 13 species occurring at elevations of 3500 m or above (Fig. 4). The Asteraceae contribute more than 60% of the alpine flora of subshrubs, with eight species. Four species of *Ericameria* (Asteraceae) and three species each of *Penstemon* (Plantaginaceae), and one Monardella (Lamiaceae) form subshrubs that reach alpine elevations. Five species are considered to be subalpine and alpine specialists based on a lower elevational limit of 2700 m or a mean elevational range above 3000 m. Four of these are members of the Asteraceae—Sphaeromeria cana (D. C. Eaton) A. Heller, Ericameria parryi (A. Gray) G. L. Nesom & G. I. Baird var. monocephala (A. Nelson & P. B. Kenn.) G. L. Nesom & G. I Baird, E. bloomer (A. gray) J. F. Macbr., and *Chrysothamnus viscidiflorus* (Hook.) Nutt. var. viscidiflorus. The two latter species have very broad elevational occurrence from 800-4000 m.

There are 23 species of woody shrubs that extend into the alpine zone of the Sierra Nevada (Fig. 4). Just four families account for the majority of the high elevation shrubs. The largest of these is the Salicaceae (eight species of Salix), followed by the Ericaceae (five species, each in a different genus), Grossulariaceae (three species of Ribes), and Rosaceae (three species, each in a different genus). The highest elevation reached is

reported for Sorbus californica at 4300 m. However, this elevation record appears to not be supported by specimen records in the Consortium of California Herbaria (ucjeps.berkeley.edu/ consortium), and therefore needs confirmation. There are six additional shrub species that reach elevations of 4000 m—Salix orestera C. K. Schneid., S. planifolia Pursh, S. petrophila Rydb., Gaultheria humifusa (Graham) Rydb., Holodiscus discolor (Pursh) Maxim. var. microphyllus (Rydb) Jeps., and *Ribes montigenum* McClatchie. Only three shrub species can be considered as subalpine and alpine specialists based on a lower elevational limit at or above 2700 m or median range of occurrence above 3000 m. These are Salix planifolia, S. brachycarpa Nutt. var. brachycarpa, and S. nivalis Hook. Three more shrub species just miss this definition of high elevation specialist. Arctostaphylos uva-ursi (L.) Spreng. has an elevational range of 2400–3300 m, while Jamesia americana Torr. & A. Gray (Hydrangeaceae) and Ribes cereum Douglas var. inebrians (Lindl.) C. L. Hitchc. are alpine species that extend down to lower elevations of 2070 m and 2100 m, respectively. Including the above species, there are a total of 39 shrub species that occur at elevations of 3300 m or above in the Sierra Nevada. This group includes two more species of Salix, one additional Ribes, five Ericaceae, three Rosaceae, two species of Caprifoliaceae, and a scattered diversity of species from other families (Appendix 2).

Five species of coniferous trees in the Pinaceae have scattered populations that extend well above typical treeline elevation on favorable sites. The treeline pines, *Pinus albicaulis* Engelm., *P. flexilis* E. James and *P. balfouriana* Grev. & Balf., all have local populations that reach as high as 3700 m in elevation in the Sierra Nevada, while *P. contorta* Loudon subsp. *murrayana* (Grev. & Balf.) Critchf. and *Tsuga mertensiana* (Bong.) Carrière reach 3500 m. Just missing the elevation of the alpine zone are scattered trees of *Pinus monticola* Douglas ex D. Don that reach up to 3400 m.

### Elevational Amplitude

Separating alpine taxa into categories of elevational ranges over which they occur provides some insight into their ecological amplitude and thus a crude measure of potential niche breadth. There are nine obligate alpine taxa in the Sierra Nevada restricted in occurrence to elevations at or above 3500 m. These are *Boechera depauperata* (A. Nelson & P. B. Kenn.) Windham & Al-Shehbaz (Brassicaceae), *Botrychium paradoxum* and *B. tunux* Stensvold & Farrar (Ophioglossaceae), *Carex incurviformis* Mack. (Cyperaceae), *Draba sierra* Sharsm. (Brassicaceae), *Eriogonum wrightii* Torr. ex Benth. var. *olanchense* 

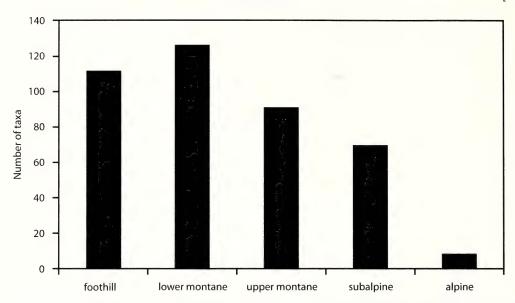


FIG. 6. Lower elevational zone of occurrence for taxa in the alpine flora of the Sierra Nevada. The elevational limits of these zones are 0–1190 m for the foothill zone, 1200–1990 m for the lower montane zone, 2000–2699 m for the upper montane zone, 2700–3490 m for the subalpine zone, and 3500 m and above for the alpine zone.

(J. T. Howell) Reveal (Polygonaceae), *Minuartia stricta* (Sw.) Hiern (Caryophyllaceae), *Phlox dispersa* Sharsm. (Polemoniaceae), and *Poa lettermanii* (Poaceae).

There an additional 67 alpine species (70 taxa, 17.2% of all taxa) with ranges restricted to the elevations of subalpine and alpine habitats at or above 2700 m (Fig. 6). Examining the floristic composition of all 76 species (79 taxa) with a range restricted to subalpine and alpine elevations, just four families comprise more than half of these. These are the Asteraceae (11 species), Brassicaceae (nine species), Rosaceae (eight species, nine taxa), and Poaceae (eight species). Three additional species would be added to the obligate subalpine and alpine flora if the elevational limit were reduced to 3300 m. These are Astragalus ravenii Barneby (Fabaceae), Carex tiogana D. W. Taylor & J. D. Mastrog. (Cyperaceae), and Chaenactis douglasii (Hook.) Hook. & Arn. var. alpina A. Gray (Asteraceae).

Looking at the level of all alpine taxa, 22.4% have a lower elevational limit in the upper montane zone (2000–2699 m) and a further 31.0% have a lower limit in the lower montane zone (1200–1999 m). Finally 27.5% of the alpine taxa have a broad elevational amplitude of occurrence extending upward from the foothill zone below 1200 m up into the alpine (Fig. 6).

Plotting the elevational amplitude of all of the alpine taxa shows a peak at about 2300 m, with relatively fewer species exhibiting very broad or very narrow elevational amplitudes (Fig. 7). Nevertheless, there are many taxa with surprising broad ranges of elevational occurrence. There are 77 species that have an elevational amplitude of

3000 m or more, and six species that have 4000 m or more of amplitude in California. These latter species, each in a different family, are Callitriche palustris (Plantaginaceae), Calyptridium umbellatum (Montiaceae), Cystopteris fragilis (Woodsiaceae), Draba cana Rydb. (Brassicaceae), Epilobium ciliatum Raf. subsp. ciliatum (Onagraceae), and Erysimum capitatum (Hook.) Greene var. capitatum (Brassicaceae). Were the elevational definition of the alpine zone lowered to 3300 m, a large number of species with broad elevational amplitudes would be added to the flora. There are 42 species in this group of added taxa that have 3000 m or more of elevational amplitude in their range of occurrence.

### Biogeography and Endemism

Within the Sierra Nevada itself, the distributions of the high elevation flora are relatively well spread between the northern, central and southern subregions of the Sierra Nevada. Assessing species reaching an elevational boundary of 3300 m, 70% of the 567 taxa occur in all three subregions. The northern subregion has 76% of the alpine flora present, while the central and southern Sierra Nevada have 90% and 88% of the alpine flora present, respectively. A number of alpine species have their southern limit of distribution in the central Sierra Nevada. These include Carex whitneyi Olney (Cyperaceae), Podistera nevadensis (A. Gray) S. Watson (Apiaceae), Claytonia megarhiza (A. Gray) S. Waston (Montiaceae), Thalictrum alpinum L. (Ranunculaceae), Galium grayanum Ehrend. var. grayanum (Rubiaceae), and Salix nivalis (Salicaceae).

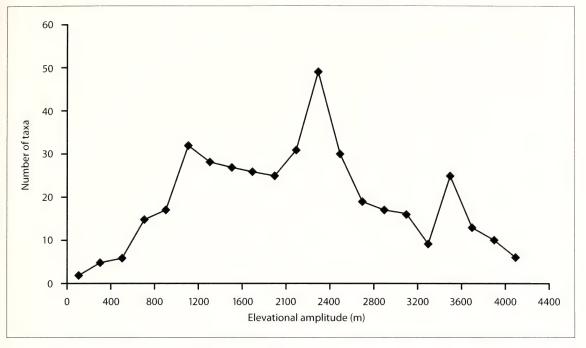


FIG. 7. Elevational amplitude of alpine taxa in the Sierra Nevada. These values are based on the range expressed from upper and lower limits of elevational distribution in California as presented in Baldwin et al. (2012).

The broader biogeographic relationships of the alpine flora at or above 3500 m indicate its diverse origins (Fig. 8). Widespread species distributed across North America and beyond as boreal or arctic-alpine taxa comprise 13.6% of the flora (Table 1). The largest group of taxa (34.3%) shows patterns of distribution as cordilleran species widespread in mountain regions of the western United States. Next in importance

are taxa with a range in the Intermountain Region of the Great Basin, comprising 20.5% of taxa. A group consisting of 15.8% of the taxa has ranges extending along the Sierra Nevada axis to the Cascade Range and often on to the Pacific Northwest.

The alpine flora of the Sierra Nevada includes 36 endemic taxa restricted in their distribution to the Sierra Nevada (Table 2). These endemic taxa

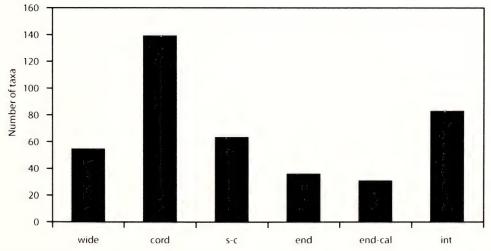


FIG. 8. Biogeographic relationships of the alpine flora of the Sierra Nevada. WIDE = widespread taxa present in many habitats or regions across North America and/or throughout the world; CORD = cordilleran taxa widespread in mountain regions of the western United States; S-C = Sierra/Cascade taxa with a Pacific Northwest distribution; END = taxa endemic to the Sierra Nevada; and END-CAL = taxa endemic to California, as broadly defined; INT = intermountain taxa present in the Great Basin. See text for discussion.

Table 1. Examples of the Broader Biogeographic Relationships of the Alpine Flora of the Sierra Nevada.

| Biogeographic range category   | Examplar taxa  |
|--|--|
| Widespread taxa distributed<br>across North America and<br>beyond as circumboreal or<br>arctic-alpine taxa | Anemone drummondii (Ranunculaceae), Carex capitata (Cyperaceae), Crepis nana (Asteraceae), Cystopteris fragilis (Woodsiaceae), Deschampsia cespitosa (Poaceae), Oxyria digyna (Polygonaceae), Phleum alpinum (Poaceae), Rhodiola integrifolium (Crassulaceae), Salix nivalis and S. petrophila (Salicaceae), Sibbaldia procumbens (Rosaceae), Trisetum spicatum (Poaceae)                              |
| Cordilleran taxa widespread in<br>mountain regions of the<br>western United States                         | Antennaria media (Asteraceae), Carex phaeocephala (Cyperaceae), Erigeron vagus (Asteraceae), Gentiana calycosa (Gentianaceae). Lewisia pygmaea (Montiaceae), Phlox condensata (Polemoniaceae), Poa glauca subsp. rupicola (Poaceae), Ribes cereum (Grossulariaceae), Stipa pinetorum (Poaceae)   |
| Intermountain Region taxa distributed across the Great Basin   | Cryptantha nubigena (Boraginaceae), Cymopterus cinerarius (Apiaceae),<br>Eriogonum incanum (Polygonaceae), Ivesia shocklevi (Rosaceae), Jamesia<br>americana (Hydrangeaceae), Podistera nevadensis (Apiaceae), Selaginella<br>watsonii (Selaginellaceae), Trifolium monanthum subsp. monanthum (Fabaceae)  |
| Taxa extending from the Pacific<br>Northwest and Cascade<br>Range  | Anelsonia eurycarpa (Brassicaceae), Astragalus whitneyi (Fabaceae), Boechera howellii (Brassicaceae), Carex breweri (Cyperaceae), Eriogonum lobbii (Polygonaceae), Gentiana newberryi (Gentianaceae), Potentilla breweri and P. flabellifolia (Rosaceae), Ranunculus alismifolius var. alismellus (Ranunculaceae), Senecio fremontii var.occidentalis (Asteraceae), Silene sargentii (Caryophyllaceae) |

are heavily weighted toward subalpine and alpine specialists, with 29 of these restricted in distribution to elevations of 2700 m or above, or with median elevational range above 3000 m. Two generic lineages are prominent among these endemics, with five taxa each of *Draba* and *Eriogonum*. Five of the alpine endemics are annual species—*Orochaenactis thysanocarpha* (A. Gray) Coville (Asteraceae), *Cryptantha circumscissa* var. *rosulata* (Boraginaceae), *Streptanthus gracilis* (Brassicaceae), and *Leptosiphon oblanceolatus* (Polemoniaceae).

The southern Sierra Nevada is the most significant subregion for endemics, with 15 of the 36 endemic taxa (42%) are restricted in distribution to the area from the Kings River drainage south that includes Kings Canyon and Sequoia National parks (Table 2). These are Draba cruciata Payson, D. longisquamosa O. E. Schulz, D. sharsmithii Rollins & R. A. Price, Eriogonum polypodum Small, E. spergulinum A. Gray var. pretense (S. Stokes) J. T. Howell, E. wrightii var. olanchense, Galium hypotrichium A. Gray subsp. *subalpinum* (Hilend & J. T. Howell) Ehrend., Leptosiphon oblanceolatus, Monardella beneolens Shevock, Ertter & Jokerst, Oreonana clementis (M. E. Jones) Jeps., Orthochaenactis thysanocarpha, Phlox dispersa, Pinus balfouriana var. austina R. J. Mastrog. & J. D. Mastrog., Streptanthus gracilis, and Trifolium kingie S. Waston subsp. dedeckerae (J. M. Gillett) D. Heller.

Another 13 taxa are restricted to the central and southern Sierra Nevada. Five of the endemics are present across the northern, central and southern subregions of the Sierra Nevada, and three endemic taxa are restricted in occurrence to the central Sierra Nevada. These are *Draba* 

sierrae, Eriogonum ovalifolium Nutt. var. caelestinum Reveal, and Lupinus gracilentus Greene (Table 2). Although the absence of peaks above 3500 m in the Sierra Nevada north of Yosemite National Park explains the lack of endemics restricted to this subregion, the scattered lower elevation alpine communities of the northern Sierra Nevada retain moderately high richness of species.

In addition to the members of the alpine flora that are endemic to the Sierra Nevada, there are an additional 31 alpine taxa that are Californian endemics, allowing for a broad interpretation of the floristic region to include the westernmost ranges of the Great Basin lying close to the Sierra Nevada and the southern Cascade Range in Oregon. Many of the Californian endemics have ranges that extend to the Sweetwater and/or White Inyo mountains, while others extend into the high Transverse and Peninsular Ranges of southern California and a small number extend into the southern Cascade Range. The pattern of dominant endemism centered in the southern Sierra Nevada is not seen among these taxa. Twelve of these occur throughout the Sierra Nevada and an additional 12 are restricted to the central and southern areas of the range, while only four species are limited to the southern Sierra Nevada.

If the lower limit of the alpine zone were dropped to 3300 m, 11 additional Sierra Nevada endemics would be added (Table 2). Four of these are restricted to the southern Sierra Nevada (Astragalus ravenii, Boechera pygmaea (Rollins) Al-Shehbaz, Castilleja praeterita Heckard & Bacig., and Phacelia orogenes), with three each present in the central and southern Sierra Nevada and in all three regions. One species is restricted

to the central Sierra Nevada. Five additional Californian endemics would be added if the lower alpine limit was dropped to 3300 m (Table 2).

### DISCUSSION

# Defining the Alpine Zone of California

Critically defining what species should be included in an alpine flora is an imperfect task given the lack of a simple operational definition, as discussed below. The high elevation areas of the Sierra Nevada broadly classified as subalpine and alpine, or upper Hudsonian and Arctic-Alpine in the Merriam life zone classification (Daubenmire 1938), would roughly include those areas lying above about 3000 m elevation (Fig. 2). Such subalpine and alpine habitats cover extensive areas of the central and southern Sierra Nevada, but only scattered areas of the northern Sierra Nevada lying north of Sonora Pass. The higher elevation area of this northern Sierran region, however, supports mosaics of subalpine forest, shrublands, and low alpine-like vegetation (Smiley 1915, 1921).

A simple definition of alpine habitat is that area occurring above treeline, with the caveat that most alpine species are not obligate in inhabiting habitats above treeline and typically occur to varying degrees at lower elevations (Packer 1974). While this approach sounds logical, timberline itself can be highly variable even in a local area depending on slope exposure, erosional history, parent material, disturbance history, and local microclimate (Billings 2000).

Sharsmith (1940) recognized the alpine flora as a distinct subdivision of the overall California flora, characterized by its geographic range, growth forms, species composition, and constancy with which the alpine association of species is maintained. Although he described the alpine zone as reaching its lower limit at an average elevation of 3500 m, the limit used in this paper, nowhere in his dissertation is there a clear statement of criteria for his inclusion of species. He stated,

While certain species are absolute indicators of the alpine flora, it is the particular association of species which gives it its characteristic. Although many species occur elsewhere, this special assemblage is not met until the alpine area is reached. Everywhere the flora presents the impression of unity, an impression reinforced by increased field experience.

The combined subalpine and alpine flora of the Sierra Nevada as defined by Smiley (1921) included 633 species, with 41 listed as indicators of the Arctic-Alpine zone. He considered 158 species to be Sierra Nevada endemics and another 20 species to be restricted in distribution to the Sierra Nevada and the southern California mountains. Sharsmith (1940) included 189 species

in his alpine flora of the Sierra Nevada, with 31 of these considered to be endemic. This flora was composed of 183 herbaceous perennials and six annual species, but did not include any woody species. A similar estimate was made by Stebbins (1982) who stated that there were 207 species in the Sierra Nevada alpine flora. Finally, a much higher estimate came from Major and Bamberg (1967) who used the species descriptions in Munz (1959) to estimate a Sierran alpine flora of about 600 species, a number similar to that reported here for taxa reaching 3300 m or above.

### Growth Forms

The relative dominance of a herbaceous perennial growth forms present in the alpine flora of the Sierra Nevada is typical of other alpine floras worldwide and does not change dramatically in a gradient from the Rocky Mountains west across the Great Basin (Billings 1978, 2000; Rundel et al. 2008). Herbaceous perennials have the characteristic of maintaining large proportions of total biomass belowground where they play an important role in carbohydrate storage over the winter months (Mooney and Billings 1960; Billings 1974). The herbaceous perennials include species with a variety of ecological forms and life history strategies of carbon allocation to belowground and aboveground vegetative, and reproductive tissues (Rundel et al. 2005), and many of these are relatively long-lived plants surviving for decades (Billings 1974; Pollak 1991).

As in other alpine regions, perennial graminoids in alpine habitats of the Sierra Nevada commonly dominate plant communities of wet meadows that dry earlier than fellfield communities. In contrast, fellfield habitats exhibit a mixed dominance of broad-leaved erect perennials, perennial graminoids, and mats and cushions (Rundel et al. 2005). Mat and cushion growth forms of herbaceous perennials are widespread in the high elevation Sierra Nevada, where the 46 taxa listed here represent 12% of the alpine flora. These are most prominent ecologically on windswept rocky slopes or other exposed areas that remain snow-free during the winter.

Because of limiting stress factors of short and severe growing conditions, annual plants are generally rare in the typical circumboreal arcticalpine floras of the Northern Hemisphere, comprising no more than 1–2% of the flora (Billings 2000). Although not abundant, annuals, nevertheless, are more common in alpine flora of the Sierra Nevada and White Mountains where they comprise about 6–8% of the floras (Jackson and Bliss 1982; Jackson 1985; Rundel et al. 2008). The species richness of alpine annual taxa, however, drops rapidly at elevations above 3300 in the Sierra Nevada (Fig. 5). Went (1948, 1953)

TABLE 2. ENDEMIC TAXA OF THE ALPINE FLORA OF THE SIERRA NEVADA, CALIFORNIA WITH THEIR UPPER RANGE OF OCCURRENCE AND GROWTH FORMS. For range: n = northern Sierra Nevada, c = central Sierra Nevada, and s = southern Sierra Nevada. For growth forms: A = annual, G = geophyte, P = erect herbaceous perennial, P-G = perennial graminoid, P-MAT = mat or cushion, SS = subshrub, T = tree. Species names follow Baldwin et al. (2012).

| Endemic group                          | Family                   | Range      | Growth form |
|--|--------------------------|------------|-------------|
| Sierra Nevada endemics >3500 m         |                          |            |             |
| Aquilegia pubescens                    | Ranunculaceae            | n,c,s      | P           |
| Calamagrostis muiriana                 | Poaceae                  | c,s        | P-G         |
| Carex congdonii                        | Cyperaceae               | c,s        | P-G         |
| Cryptantha circumscissa var. rosulata  | Boraginaceae             | n,c,s      | A           |
| Dodecatheon subalpinum                 | Primulaceae              | c,s        | P           |
| Draba cruciata                         | Brassicaceae             | s          | P           |
| Draba lemmonii                         | Brassicaceae             | n,c,s      | P           |
| Draba longisquamosa                    | Brassicaceae             | S          | P           |
| Draba sharsmithii                      | Brassicaceae             | S          | P           |
| Draba sierrae                          | Brassicaceae             | c          | P-MAT       |
| Eriogonum nudum var. scapigerum        | Polygonaceae             | c,s        | P           |
| Eriogonum ovalifolium var. caelestinum | Polygonaceae             | c          | P-MAT       |
| Eriogonum polypodum                    | Polygonaceae             | S          | P-MAT       |
| Eriogonum spergulinum var. pratense    | Polygonaceae             | S          | P           |
| Eriogonum wrightii var olanchense      | Polygonaceae             | S          | P-MAT       |
| Galium hypotrichium subsp. subalpinum  | Rubiaceae                | S          | P           |
| Hazardia whitneyi var. whitneyi        | Asteraceae               | n,c,s      | SS          |
| Ivesia muirii                          | Rosaceae                 | c,s        | P           |
| Ivesia pygmaea                         | Rosaceae                 | c,s        | P           |
| Leptosiphon oblanceolatus              | Polemoniaceae            | s          | Α           |
| Lewisia disepala                       | Montiaceae               | c,s        | P           |
| Lupinus covillei                       | Fabaceae                 | c,s        | P           |
| Lupinus gracilentus                    | Fabaceae                 | c          | P           |
| Luzula orestera                        | Juncaceae                | n,c,s      | P-G         |
| Monardella beneolens                   | Lamiaceae                | s          | SS          |
| Oreonana clementis                     | Apiaceae                 | S          | P           |
| Oreostemma peirsonii                   | Asteraceae               | c,s        | P           |
| Orochaenactis thysanocarpha            | Asteraceae               | s          | Α           |
| Phlox dispersa                         | Polemoniaceae            | S          | P-MAT       |
| Pinus balfouriana var. austrina        | Pinaceae                 | S          | T           |
| Poa stebbinsii                         | Poaceae                  | c,s        | P-G         |
| Polemonium eximium                     | Polemoniaceae            | c,s        | P           |
| Stipa kingii                           | Poaceae                  | c,s        | P-G         |
| Streptanthus gracilis                  | Brassicaceae             | s          | Α           |
| Trichophorum clementis                 | Cyperaceae               | c,s        | P-G         |
| Trifolium kingii subsp. dedeckerae     | Fabaceae                 | s          | P           |
| Sierra Nevada endemics 3300–3499 m     |                          |            |             |
| Astragalus ravenii                     | Fabaceae                 | S          | P           |
| Boechera pygmaea                       | Brassicaceae             | S          | P           |
| Castilleja praeterita                  | Orobanchaceae            | s<br>s     | P           |
| Erigeron elmeri                        | Asteraceae               | c,s        | P           |
| Hulsea vestita subsp. vestita          | Asteraceae               | c,s        | P           |
| Ipomopsis aggregata subsp. bridgesii   | Polemoniaceae            |            | P           |
| Lilium kelleyanum                      | Liliaceae                | c,s<br>c,s | G           |
| <b>=</b>                               |                          |            | P           |
| Lomatium torreyi<br>Phacelia eisenii   | Apiaceae<br>Boraginaceae | n,c,s      | A           |
| Phacelia orogenes                      | Boraginaceae             | c,s<br>s   | A           |
| Trifolium monanthum subsp. tenerum     | Fabaceae                 | n,c,s      | P           |
|  | 1 abaccac                | 11,0,5     |             |
| Californian endemics >3500             | T. 1                     |            | D 3 4 4 77  |
| Astragalus kentrophyta var. danaus     | Fabaceae                 | c,s        | P-MAT       |
| Carex mariposana                       | Cyperaceae               | n,c,s      | P-G         |
| Castilleja nana                        | Orobanchaceae            | n,c,s      | P           |
| Chaenactis alpigena                    | Asteraceae               | n,c,s      | P-MAT       |
| Delphinium polycladon                  | Ranunculaceae            | n,c,s      | P           |
| Draba breweri                          | Brassicaceae             | n,c,s      | P           |
| Draba subumbellata                     | Brassicaceae             | S          | P-MAT       |
| Eriogonum gracilipes                   | Polygonaceae             | c,s        | P-MAT       |
| Eriogonum umbellatum var. covillei     | Polygonaceae             | c,s        | P-MAT       |

TABLE 2. CONTINUED.

| Endemic group                              | Family         | Range | Growth form |
|--|----------------|-------|-------------|
| Galium hypotrichium subsp. hypotrichium    | Rubiaceae      | c,s   | P           |
| Hulsea vestita subsp. pygmaea              | Asteraceae     | c,s   | P           |
| Ivesia lycopodioides subsp. lycopodioides  | Rosaceae       | n,c   | P           |
| Ivesia lycopodioides subsp. scandularis    | Rosaceae       | c,s   | P           |
| Ivesia santolinoides                       | Rosaceae       | n,c,s | P           |
| Lewisia glandulosa                         | Montiaceae     | c,s   | P           |
| Lupinus breweri var. breweri               | Fabaceae       | n,c,s | P-MAT       |
| Lupinus breweri var. bryoides              | Fabaceae       | S     | P-MAT       |
| Lupinus latifolius var. parishii           | Fabaceae       | c,s   | P           |
| Lupinus lepidus var. ramosus               | Fabaceae       | c,s   | P           |
| Lupinus padre-crowleyi                     | Fabaceae       | S     | P-MAT       |
| Lupinus pratensis var. pratensis           | Fabaceae       | c,s   | P           |
| Phyllodoce breweri                         | Ericaceae      | n,c,s | S           |
| Poa keckii                                 | Poaceae        | n.c.s | P-G         |
| Potentilla pseudosericea                   | Rosaceae       | c,s   | P           |
| Potentilla wheeleri                        | Rosaceae       | S     | P           |
| Primula suffrutescens                      | Primulaceae    | n,c,s | P           |
| Ranunculus eschscholtzii var. oxynotus     | Ranunculaceae  | n,c,s | P           |
| Tonestus peirsonii                         | Asteraceae     | С     | P           |
| Triteleia dudleyi                          | Themidaceae    | c,s   | G           |
| Viola pinetorum subsp. grisea              | Violaceae      | n,c,s | P           |
| Viola purpurea subsp. mesophyta            | Violaceae      | n,c,s | P           |
| Californian endemics 3300–3499 m           |                |       |             |
| Eriogonum latens                           | Polygonaceae   | c,s   | P           |
| Frasera puberulenta                        | Gentianaceae   | c,s   | P           |
| Hordeum brachyantherum subsp. californicum | Poaceae        | n,c,s | P-G         |
| Penstemon caesius                          | Plantaginaceae | S     | SS          |
| Plagiobothrys torreyi var. diffusus        | Boraginaceae   | n,c,s | A           |

suggested that many of the high elevation annuals in the Sierra Nevada were related to desert species.

Severe winter conditions typically limit the occurrence of woody plants above treeline, with prostrate mats and cushions as prominent exceptions. The upright growth form of woody shrubs and krummholtz tree species exposes their tissues to extreme conditions of temperature and wind exposure (Körner 2003). This impact on shrub occurrence can be seen in Fig. 5 where shrub richness in the Sierra Nevada drops sharply with increasing elevation above 3300 m, similar to the pattern for annual species. Much of the alpine flora of woody species comes from species of *Salix* and members of the Ericaceae, groups which favor moist habitats with some level of protection.

# Biogeography and Endemism

The alpine flora of mountain ranges on the western margin of the Great Basin of California and western Nevada exhibit very strong relationships to that of the Sierra Nevada (Rundel et al. 2008). The Sweetwater Mountains supports a flora of 173 species in 16 km² of alpine habitat, with 94% of this flora common to the Sierra Nevada (Hunter and Johnson 1983). The Wassuk Range has an alpine flora of 70 species in just 2.6 km² of alpine habitat (Bell and Johnson 1980). Again, this flora is has stronger floristic

relationships to the Sierra Nevada than the Rocky Mountains.

As with the Sweetwater Mountains and Wassuk Ranges, the flora of the White Mountains exhibits much stronger floristic relationships to the Sierra Nevada than to the Rocky Mountains. About 90% of the species in the alpine flora of the White Mountains are also found in the Sierra Nevada (Rundel et al. 2008), compared with only 58% that occur in the ranges of the central Rocky Mountains (Scott 1995). These values are significantly higher for both ranges than earlier estimates made on incomplete data (Lloyd and Mitchell 1973).

Mountain ranges in the central Great Basin generally show strong floristic linkages to the Rocky Mountains and weaker links to the Sierra Nevada (Billings 1978). Loope (1969) reported 189 alpine species from the Ruby Mountains in northeastern Nevada, with this flora heavily linked to the Rocky Mountains. The isolated San Francisco Mountains in Arizona with only 5.2 km² of alpine habitat has 80 species, and likewise shows strong floristic relationships to the Rocky Mountains despite its separation of about 200 km (Schaak 1983).

The level of endemism in the alpine Sierra Nevada flora is a relatively small part of the overall endemism for the montane and higher parts of the range. Based on current information, there are 205 taxa endemic to what *The Jepson* 

Manual (Hickman 1993) classifies as the northern, central, and southern high Sierra Nevada, i.e., the montane, subalpine and alpine zones above foothill habitats (R. Moe, Univ. of California, Berkeley, personal communication). The 36 Sierran endemics present in the alpine flora would thus comprise 18% of the endemic flora of the higher Sierra Nevada.

The unique California component of the alpine flora of the Sierra Nevada is considerably greater if one considers the endemic component of 31 species in the alpine flora that are not uniquely limited to the Sierra Nevada but are Californian endemics as defined earlier. Combining the endemic taxa with Sierran and Californian limits of distribution, the total of 66 taxa represents 16% of the alpine flora. This is a relatively high figure compared to other alpine ranges in continental North America and Europe, and reflects the environmental stress conditions associated with the summer-dry mediterranean-type climate present in the Sierra Nevada.

Stebbins (1982) analyzed the flora of the high Sierra Nevada, defined similarly to that of Smiley (1921) as the upper montane to alpine zones, and identified 119 endemic species, 13.5% of the total flora. He further noted that another 60% of the flora extended beyond the Sierra Nevada only as far as southern California, western Nevada, and southern Oregon.

Raven and Axelrod (1978) briefly discussed the diversity and evolution of the subalpine and alpine flora of the Sierra Nevada, listing 68 endemics for this region. Their table of endemics, however, is outdated by more recent information on distribution patterns and species concepts. Shevock (1996) gave a figure of 405 endemic taxa of vascular plants for the entire Sierra Nevada. The 36 alpine endemics reported here would comprise 9% of this total. Of the three geographical subregions (northern, central, and southern) of the entire range, the southern Sierra Nevada is the richest in endemics, rare species, and total floristic composition (Shevock 1996), a finding similar to that reported here.

## The Evolution of the Sierran Alpine Flora

A detailed assessment of the biogeographic and evolutionary origin of the alpine flora of the Sierra Nevada is beyond the scope of this review. Broad interpretations of biogeographic relationships within alpine lineages have been discussed by previous authors (e.g., Smiley 1921; Sharsmith 1940; Chabot and Billings 1972; Taylor 1977; Major and Taylor 1977; Raven and Axelrod 1978; Stebbins 1982) but recent phylogenetic studies have made many of these earlier interpretations subject to re-evaluation.

Evidence for a north to south route of colonization of high mountain areas of the Sierra

Nevada comes from a pattern of decreasing presence of Rocky Mountain floristic elements and an increasing number of endemics alpine species as one moves from the northern to southern crest of the range (Chabot and Billings 1972; Raven and Axelrod 1978). The southern limit of a number of alpine species on Mount Lassen suggests the possibility that some of these and other Cascade Range species may well have been present in the Sierra Nevada in the late Pliocene or early Pleistocene. Although the species composition of lower and middle elevation conifer forests of Lassen National Park are strongly related to that of the Sierra Nevada, the summits of the highest peaks in Lassen support an alpine flora that exhibits stronger floristic links to Mount Shasta and the Cascade Range to the north (Gillett et al. 1995). Alpine species with disjunct patterns of distribution from Mount Lassen to the Cascade Range volcanoes include Cardamine bellidifolia L. (Brassicaceae), Carex illota L. H. Bailey (Cyperaceae), Collomia larsenii (A. Gray) Payson (Polemoniaceae), Draba aureola S. Watson (Brassicaceae), Erigeron elegantulus Greene and E. nivalis Nutt. (Asteraceae), Hulsea nana A. Gray (Asteraceae), Polemonium pulcherrimum Hook. var. pilosum (Greenm.) Brand (Polemoniaceae), and Silene suksdorfii B. L. Rob. (Caryophyllaceae). The Klamath Mountains also mark the southern distribution limit of a number of boreal species that do not occur in the high elevations of the Sierra Nevada (Howell 1944).

Alpine and subalpine species characteristic of wet meadows and other moist sites typically have broad geographic ranges but become increasing habitat specific moving to the south in the Sierra Nevada as precipitation decreases (Kimball et al. 2004; Moore et al. 2007). The relative isolation of the Sierra Nevada from northern ranges and the summer-dry have clearly acted as a filter to exclude some widespread circumpolar arcticalpine species such as Dryas integrifolia Vahl (Rosaceae) and Silene acaulis L. (Caryophyllaceae) which do not occur anywhere in California. Species growing in xeric rocky habitats show higher levels of endemism and smaller range size due to isolation and divergence from ancestral populations distributed in wetter habitats to the north.

More controversial, however, is the origin of disjunct Rocky Mountain species present in the central and southern Sierra Nevada, often growing in azonal soil conditions. There is both geological and paleobotanical evidence to suggest that the mean elevation of the Great Basin was as much as 1500 m higher in the Miocene and that the current Basin and Range topography is the result of subsidence rather than uplift (Wernicke et al. 1988; Wolfe et al. 1997). The presence of higher elevations in the Great Basin during the

Pleistocene could possibly have provided stepping stones to allow the dispersal of alpine organisms from the east (Major and Bamberg 1967; Taylor 1976a). Molecular evidence indicates that at least one lineage of butterflies entered the Sierra Nevada by this route (Nice and Shapiro 2001). However, other authors feel that the majority of these disjunct plant species reached the Sierra Nevada by the same dominant route from the Western Cordillera via the Cascade Range and south (Chabot and Billings 1972).

Modes of speciation in the development of the endemic alpine flora of the Sierra Nevada are clearly complex. Polyploidy and associated apomixis are widely recognized as major factors in plant evolution, and these factors have had a relatively recent impact on speciation in producing stable self-propagating lineages (Soltis et al. 2009). In the alpine region of the Sierra Nevada, as in other alpine regions, diploid lineages of polyploid complexes often occupy unglaciated areas and resist introgression due hypothetically to a significantly higher seed set. However, asexual apomictic populations are more widespread than their sexual relatives in glaciated areas. Sexual and asexual polyploids may become distinct stabilized species through hybrid origin.

Reproductive isolation and stability of tetraploids within their respective distribution as well as the value of uniparental reproduction provide the advantages of apomixis. Many important genera in the alpine flora of the Sierra Nevada are notable for the presence of apomixis, with *Boechera* (Schranz et al. 2005; Dobes et al. 2007), *Draba* (Jordon-Thaden and Koch 2008), and *Antennaria* (Bayer and Stebbins 1987) as examples. Additional speciose genera in the Sierra Nevada known to have complex apomictic populations include *Arnica* and *Crepis* (Asteraceae; Noyes 2007), *Poa* and *Calamagrostis* (Poaceae), and *Potentilla* (Rosaceae) (Asker and Jerling 1992).

Other modes of alpine speciation have also been described for the Sierra Nevada. Some speciation, for example, has hypothetically come from lowland arid-adapted taxa colonizing the glaciated terrain of the range at the end of the Pleistocene (Went 1948, 1953). Speciation has also been shown to be the result of population disjunction and reproductive isolation (Chase and Rayen 1975).

Although the Transverse and Peninsular ranges are well separated from the higher elevations of the Sierra Nevada, more than one third of the Sierran alpine flora has a range of distribution that extends to these southern California ranges. While some of these species occur at lower elevations, others are typically subalpine and alpine species that must have crossed the Mojave Desert during the cold conditions of the Pleisto-

cene. This latter group includes Androsace septentrionalis (Primulaceae), Hulsea vestita A. Gray subsp. pygmaea (A. Gray) Wilken (Asteraceae), Oxyria digyna (L.) Hill (Polygonaceae), and Podistera nevadensis (Apiaceae).

There are lessons to be learned from recent studies of the patterns of diversification in the European alpine flora. These strongly demonstrate that speciation have been promoted by diverse ecological, evolutionary, and life history traits related to population structure, phylogenetic relationships, breeding system, dispersal syndromes, ecophysiological ranges of habitat requirements, and competitive abilities (Comes and Kadereit 1998; Taberlet et al. 1998; Hewitt 2000; Gugerli and Holderegger 2001; Vargas 2003). The complex and dynamic climatic and geological history of the Sierra Nevada operating on such traits suggests that there have been a range of different colonization and extinction histories that are species specific. Much more work on the comparative phylogeography of alpine plants in the Sierra Nevada will be necessary before we understand all of the factors responsible for present distributions and predominant modes of speciation in the alpine flora of the range.

### Research Needs

There is little doubt that the stability of the ecotone between alpine and treeline ecosystems in the Sierra Nevada and other high mountain regions has been and continues to be a function of complex interactions, with multiple drivers operating across diverse scales of time and space. This ecotone has been highly dynamic in the past and given the importance of temperature in controlling the elevation of treeline and higher alpine ecosystems, this ecotone and associated species are likely to be particularly sensitive to climate change in the future (Lloyd and Graumlich 1997; Graumlich et al. 2005; Grabherr et al. 2010). Beyond treeline studies, the expansion of woody shrub species into alpine habitats has been shown to also be a sensitive indicator of potential climate change, with significant feedbacks on microclimate and soil ecosystems (Hallinger et al. 2010), as well as species facilitation (Callaway et al. 2002). The potential sensitivity of alpine ecosystems to climate change has been the stimulus for establishing the worldwide research program Global Observation Research Initiative in Alpine Environments (GLORIA, http://www. gloria.ac.at) with the aim of providing long-term observations on the state and dynamics of alpine biota.

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APPENDIX 1. Annotated checklist of the alpine flora of the Sierra Nevada, including all taxa reaching an elevation of 3500 m. Lower and upper elevations limits are those for all of California and taken from Baldwin et al. (2012). Growth form abbreviations are: P = erect broad-leaved perennial; G = geophytes; P-G = graminoid perennial; P-MAT = mat or cushion; A = annual; Q = aquatic perennial; SS = subshrub; S = woody shrub; and T = tree. Biogeographic relationships are abbreviated as follows: WIDE = widespread taxa present in many habitats or regions across North America and/or throughout the world; CORD = cordilleran taxa widespread in mountain regions of the western North America; S-C = Sierra/Cascade taxa with a Pacific Northwest distribution; INT = intermountain taxa present in the Great Basin; END = taxa endemic to the Sierra Nevada; and END-CAL = taxa endemic to California, as broadly defined in the text. Species names follow Baldwin et al. (2012).

| Specific or   Lower   Upper   Growth   Biogeographic relationship  | 1               |                             |               |               |      |                |  |  |
|--|-----------------|-----------------------------|---------------|---------------|------|----------------|--|--|
| PTERIDOPHYTA   |                 |                             |               |               |      | Biogeographic  |  |  |
| Ophioglossaceae         Botrychium crenulatum         1500         3600         P         CORD           Ophioglossaceae         Botrychium inware         2500         4000         P         CORD           Ophioglossaceae         Botrychium simplex var.         1500         3800         P         WIDE           Ophioglossaceae         Botrychium simplex var.         1500         3800         P         WIDE           Perlacaeae         Pellaca breweri         1500         3700         P         WIDE           Petridaceae         Pellaca breweri         1500         3700         P         INT           Selaginellaceae         Selaginella watsonii         1350         4100         P         INT           Woodsiaceae         Altyrium distentifolium var.         1700         3700         P         WIDE           Woodsiaceae         Woodsia scopulina         1300         3500         P         WIDE           Pinaceae         Pinus abljouriana var.         2700         3700         T         END           Pinaceae         Pinus faviliana         120         3500         T         S-C           MONOCOTYLEDONAE         Alliane obtusum var. obtusum         1500         3500         G   |                 |                             | elevation (m) | elevation (m) | form | relationship   |  |  |
| Ophicglossaceae         Botrychium lineare         2500         4000         P         CORD           Ophicglossaceae         Botrychium simplex var.         1500         3800         P         WIDE           Ophicglossaceae         Botrychium simplex var.         1500         3800         P         WIDE           Peridaceae         Botrychium tumax         3600         3600         P         INT           Peridaceae         Pellaea breweri         1500         3700         P         INT           Selaginellaceae         Pellaea breweri         1500         3700         P         INT           Woodsiaceae         Althyrium distentifolium var.         1700         3700         P         WIDE           Woodsiaceae         Woodsiaceae         Cystopteris fragilis         50         4100         P         CORD           Woodsiaceae         Woodsiaceae         Woodsiaceae         Woodsiaceae         Woodsiaceae         Woodsiaceae         Woodsiaceae         Woodsiaceae         Woodsiaceae         WIDE           Pinaceae         Pinus dibicaulis         2135         3700         T         CORD           Pinaceae         Pinus baljouriana var.         2700         3700         T         CORD   | PTERIDOPHYTA    | A                           |               |               |      |                |  |  |
| Ophicglossaceae         Botrychium lineare         2500         4000         P         CORD           Ophicglossaceae         Botrychium spradoxum         4000         4200         P         WIDE           Ophicglossaceae         Botrychium simplex var.         1500         3800         P         WIDE           Peridaceae         Botrychium tunux         3600         3600         P         INT           Petridaceae         Pellace breweri         1500         3700         P         INT           Selaginellaceae         Pellace breweri         1500         3700         P         INT           Woodsiaceae         Althyrium distentifolium var.         1700         3700         P         WIDE           Woodsiaceae         Woodsiaceae         Woodsiaceae in Cystopteris fragilis         50         4100         P         CORD           Woodsiaceae         Woodsiaceae         Woodsiaceae in Cystopteris fragilis         50         4100         P         CORD           Pinaceae         Pinus dibicaulis         2135         3700         T         CORD           Pinaceae         Pinus baljouriana var.         2700         3700         T         CORD           Pinaceae         Pinus baljouriana var.  | Ophioglossaceae | Botrychium crenulatum       | 1500          | 3600          | P    | CORD           |  |  |
| Ophioglossaceae         Borrychium simplex var.         1500         3800         P         WIDE           Ophioglossaceae         Pellaea breweri         1500         3600         P         WIDE           Pteridaceae         Pellaea breweri         1500         3700         P         INT           Selaginellaceae         Athyvium distentifolium var.         1700         3700         P         WIDE           Woodsiaceae         Cystopteris fragilis         50         4100         P         CORD           Woodsiaceae         Woodsiaceae         Woodsiaceae Woodsia scopulma         1300         3500         P         WIDE           CONIFERAE         Pinus albicaulis         2135         3700         T         CORD           Pinaceae         Pinus salbicaulis         2135         3700         T         CORD           Pinaceae         Pinus baljouriana var.         2700         3700         T         END           Pinaceae         Pinus baljouriana var.         2700         3700         T         CORD           Pinaceae         Pinus baljouriana var.         2700         3700         T         CORD           Pinaceae         Pinus baljouriana var.         2700         3700         T  |                 |                             | 2500          | 4000          | P    | CORD           |  |  |
| Ophioglossaceae         Borrychium tumux         3600         P         WIDE           Pleridaceae         Borrychium tumux         1500         3700         P         INT           Selaginellaceae         Pellaea breweri         1500         3700         P         INT           Selaginellaceae         Albryimin distentifolium var.         1700         3700         P         WIDE           Woodsiaceae         Cystopteris fragilis         50         4100         P         CORD           Woodsiaceae         Woodsia scopulina         1300         3500         P         WIDE           CONIFERAE         Woodsiaceae         Pimus albicaulis         2135         3700         T         CORD           Pinaceae         Pinus balfouriana var.         2700         3700         T         END           Pinaceae         Pimus balfouriana var.         2700         3700         T         CORD           Pinaceae         Pimus contorta subsp.         1525         3500         T         S-C           MONOCOTYLEDONAE         T         SC         T         S-C           Alliaceae         Alliamo obrusum var. obrusum         1500         3500         T         S-C           Cyperaceae   |                 | Botrychium paradoxum        | 4000          | 4200          |      | CORD           |  |  |
| Ophioglossaceae         Batrychium tunux         3600         3600         P         WIDE           Pletridaceae         Pellae breweri         1500         3700         P         INT           Selaginellaceae         Adhyrium distentifolium var.         1700         3700         P         WIDE           Woodsiaceae         Adhyrium distentifolium var.         1700         3700         P         WIDE           Woodsiaceae         Cystopteris fragilis         50         4100         P         CORD           Woodsiaceae         Woodsia scopulma         1300         3500         P         WIDE           CONIFERAE           Pinus albicaulis         2135         3700         T         CORD           Pinus ceae         Pinus balfourian var.         2700         3700         T         END           Pinaceae         Pinus balfourian var.         2700         3700         T         SC           Pinaceae         Pinus plexilis         2600         3700         T         SC           Pinaceae         Pinus flexilis         2600         3700         T         SC           Alliaceae         Allium obtusum var. obtusum   | Ophioglossaceae |                             | 1500          | 3800          | P    | WIDE           |  |  |
| Petridaceae   Pellaea breweri   1500   3700   P   INT  | Ophioglossaceae |                             | 3600          | 3600          | P    | WIDE           |  |  |
| Woodsiaceae         Athyrium distentifolium var. americanum         1700         3700         P         WIDE americanum           Woodsiaceae         Cystopteris fragilis         50         4100         P         CORD           Woodsiaceae         Woodsia scopulina         1300         3500         P         WIDE           CONIFERAE         Pinaceae         Pinus albicaulis         2135         3700         T         CORD           Pinaceae         Pinus baljouriana var.         2700         3700         T         END           murrayana         1         2600         3700         T         CORD           Pinaceae         Pinus flexilis         2600         3700         T         CORD           Pinaceae         Chus flexilis         2600         3700         T         CORD           Vaperaceae         Carex albonigra         3000         4200         P-G         CORD <td< td=""><td></td><td></td><td>1500</td><td>3700</td><td>P</td><td>INT</td></td<>   |                 |                             | 1500          | 3700          | P    | INT            |  |  |
| Moodsiaceae  | Selaginellaceae | Selaginella watsonii        | 1350          | 4100          | P    | INT            |  |  |
| Woodsiaceae         Cystopteris fragilis         50         4100         P         CORD           Woodsiaceae         Woodsia scopulina         1300         3500         P         WIDE           CONIFERAE           Pinaceae         Pinus albicaulis         2135         3700         T         CORD           Pinaceae         Pinus balfouriana var.         2700         3700         T         END           Pinaceae         Pinus contorta subsp.         1525         3500         T         S-C           Pinaceae         Pinus flexilis         2600         3700         T         CORD           Pinaceae         Pinus flexilis         2600         3700         T         CORD           Pinaceae         Tsuga mertensiana         1200         3500         T         S-C           MONOCOTYLEDONAE         T         CORD         T         CORD           Alliaceae         Allium obtusum var. obtusum         1500         3500         G         INT           Cyperaceae         Carex albonigra         3000         4200         P-G         CORD           Cyperaceae         Carex opendonii         2600         3900         P-G         CORD           Cyperace   | Woodsiaceae     |                             | 1700          | 3700          | P    | WIDE           |  |  |
| Woodsiaceae         Woodsia scopulina         1300         3500         P         WIDE           CONIFERAE         Pinuse ablicaulis         2135         3700         T         CORD           Pinaceae         Pinus balfouriana var.         2700         3700         T         END           Pinaceae         Pinus contorta subsp.         1525         3500         T         S-C           Pinaceae         Pinus plexilis         2600         3700         T         CORD           Pinaceae         Pinus plexilis         2600         3700         T         CORD           Pinaceae         Pinus plexilis         2600         3700         T         CORD           Pinaceae         Pinus plexilis         2600         3500         T         S-C           MONOCOTYLEDONAE         Alliaceae         Alliun obtusum var. obtusum         1500         3500         G         INT           Cyperaceae         Carex albonigra         3000         4200         P-G         CORD           Cyperaceae         Carex capitata         1200         3900         P-G         WIDE           Cyperaceae         Carex deflexa var. boottii         0         3800         P-G         CORD   | Woodsiaceae     |                             | 50            | 4100          | P    | CORD           |  |  |
| CONIFERAE   Pinas albicaulis   2135   3700   T   CORD  |                 |                             |               |               |      |                |  |  |
| Pinaceae   |                 |                             |               |               |      |                |  |  |
| Pinaceae   Pinus contorta subsp.   1525   3500   T   S-C   | Pinaceae        | Pinus albicaulis            | 2135          | 3700          | T    | CORD           |  |  |
| Pinaceae   | Pinaceae        |                             | 2700          | 3700          | T    | END            |  |  |
| Pinaceae         Pinus flexilis         2600         3700         T         CORD           Pinaceae         Tsuga mertensiana         1200         3500         T         S-C           MONOCOTYLEDONAE         Section of the stant of th | Pinaceae        | Pinus contorta subsp.       | 1525          | 3500          | T    | S-C            |  |  |
| MONOCOTYLEDONAE         Alliaceae         Allium obtusum var. obtusum         1500         3500         G         INT           Cyperaceae         Carex albonigra         3000         4200         P-G         CORD           Cyperaceae         Carex breweri         2000         3900         P-G         S-C           Cyperaceae         Carex congdonii         2600         3900         P-G         END           Cyperaceae         Carex deflexa var. boottii         0         3800         P-G         CORD           Cyperaceae         Carex deflexa var. boottii         0         3800         P-G         CORD           Cyperaceae         Carex deflexa var. boottii         0         3800         P-G         CORD           Cyperaceae         Carex haydeniana         2400         3700         P-G         CORD           Cyperaceae         Carex haydeniana         2400         4200         P-G         CORD           Cyperaceae         Carex haydeniana         2400         4200         P-G         CORD           Cyperaceae         Carex heteroneura         1300         4000         P-G         CORD           Cyperaceae         Carex hoodii         650         3600         P-G <t< td=""><td>Pinaceae</td><td></td><td>2600</td><td>3700</td><td>T</td><td>CORD</td></t<>   | Pinaceae        |                             | 2600          | 3700          | T    | CORD           |  |  |
| Alliaceae  |                 | Tsuga mertensiana           | 1200          | 3500          | T    | S-C            |  |  |
| Cyperaceae         Carex albonigra         3000         4200         P-G         CORD           Cyperaceae         Carex breweri         2000         3900         P-G         S-C           Cyperaceae         Carex congdonii         2600         3900         P-G         END           Cyperaceae         Carex deflexa var. boottii         0         3800         P-G         CORD           Cyperaceae         Carex douglasii         300         3800         P-G         CORD           Cyperaceae         Carex fullfolia var. erostrata         1500         3700         P-G         CORD           Cyperaceae         Carex haydeniana         2400         4200         P-G         CORD           Cyperaceae         Carex helleri         2400         4100         P-G         S-C           Cyperaceae         Carex hendenia         1300         4000         P-G         CORD           Cyperaceae         Carex hoodii         650         3600         P-G         CORD           Cyperaceae         Carex honosii         900         3500         P-G         CORD           Cyperaceae         Carex lenticularis var.         0         3600         P-G         CORD           Cypera  | MONOCOTYLEI     | DONAE                       |               |               |      |                |  |  |
| Cyperaceae         Carex breweri         2000         3900         P-G         S-C           Cyperaceae         Carex capitata         1200         3900         P-G         WIDE           Cyperaceae         Carex capitata         1200         3900         P-G         END           Cyperaceae         Carex deflexa var. boottii         0         3800         P-G         CORD           Cyperaceae         Carex douglasii         300         3800         P-G         CORD           Cyperaceae         Carex douglasii         300         3800         P-G         CORD           Cyperaceae         Carex follolia var. erostrata         1500         3700         P-G         CORD           Cyperaceae         Carex helleri         2400         4200         P-G         CORD           Cyperaceae         Carex helleri         2400         4100         P-G         S-C           Cyperaceae         Carex helleri         2400         4100         P-G         CORD           Cyperaceae         Carex helleri         2400         4100         P-G         CORD           Cyperaceae         Carex incurviformis         3700         4000         P-G         CORD           Cyperaceae  | Alliaceae       | Allium obtusum var. obtusum | 1500          | 3500          | G    | INT            |  |  |
| Cyperaceae         Carex capitata         1200         3900         P-G         WIDE           Cyperaceae         Carex congdonii         2600         3900         P-G         END           Cyperaceae         Carex deflexa var. boottii         0         3800         P-G         CORD           Cyperaceae         Carex douglasii         300         3800         P-G         CORD           Cyperaceae         Carex filifolia var. erostrata         1500         3700         P-G         CORD           Cyperaceae         Carex haydeniana         2400         4200         P-G         CORD           Cyperaceae         Carex helleri         2400         4100         P-G         S-C           Cyperaceae         Carex helleri         2400         4100         P-G         S-C           Cyperaceae         Carex helleri         2400         4000         P-G         CORD           Cyperaceae         Carex helleri         1300         4000         P-G         CORD           Cyperaceae         Carex incurviformis         3700         4000         P-G         CORD           Cyperaceae         Carex lenticularis var.         0         3600         P-G         CORD <td< td=""><td>Cyperaceae</td><td>Carex albonigra</td><td>3000</td><td>4200</td><td>P-G</td><td>CORD</td></td<>  | Cyperaceae      | Carex albonigra             | 3000          | 4200          | P-G  | CORD           |  |  |
| Cyperaceae         Carex congdonii         2600         3900         P-G         END           Cyperaceae         Carex deflexa var. boottii         0         3800         P-G         CORD           Cyperaceae         Carex douglasii         300         3800         P-G         CORD           Cyperaceae         Carex haydeniana         2400         4200         P-G         CORD           Cyperaceae         Carex helleri         2400         4100         P-G         S-C           Cyperaceae         Carex helleri         2400         4000         P-G         INT           Cyperaceae         Carex helleri         2400         4000         P-G         INT           Cyperaceae         Carex hoodii         650         3600         P-G         CORD           Cyperaceae         Carex incurviformis         3700         4000         P-G         CORD           Cyperaceae         Carex incurviformis         3700         4000         P-G         CORD           Cyperaceae         Carex incurviformis         3700         4000         P-G         CORD           Cyperaceae         Carex leporinella         1900         3600         P-G         CORD           Cyperaceae<  | Cyperaceae      |                             | 2000          | 3900          | P-G  | S-C            |  |  |
| Cyperaceae         Carex congdonii         2600         3900         P-G         END           Cyperaceae         Carex deflexa var. boottii         0         3800         P-G         CORD           Cyperaceae         Carex douglasii         300         3800         P-G         CORD           Cyperaceae         Carex haydeniana         2400         4200         P-G         CORD           Cyperaceae         Carex helleri         2400         4100         P-G         S-C           Cyperaceae         Carex helleri         2400         4000         P-G         INT           Cyperaceae         Carex helleri         2400         4000         P-G         INT           Cyperaceae         Carex hoodii         650         3600         P-G         CORD           Cyperaceae         Carex incurviformis         3700         4000         P-G         CORD           Cyperaceae         Carex incurviformis         3700         4000         P-G         CORD           Cyperaceae         Carex incurviformis         3700         4000         P-G         CORD           Cyperaceae         Carex leporinella         1900         3600         P-G         CORD           Cyperaceae<  | Cyperaceae      | Carex capitata              | 1200          | 3900          | P-G  | WIDE           |  |  |
| Cyperaceae         Carex douglasii         300         3800         P-G         CORD           Cyperaceae         Carex filifolia var. erostrata         1500         3700         P-G         CORD           Cyperaceae         Carex haydeniana         2400         4200         P-G         CORD           Cyperaceae         Carex helleri         2400         4100         P-G         S-C           Cyperaceae         Carex heteroneura         1300         4000         P-G         INT           Cyperaceae         Carex heteroneura         1300         4000         P-G         CORD           Cyperaceae         Carex hoodii         650         3600         P-G         CORD           Cyperaceae         Carex incurviformis         3700         4000         P-G         CORD           Cyperaceae         Carex ienticularis var.         0         3600         P-G         CORD           Cyperaceae         Carex leporinella         1900         4000         P-G         CORD           Cyperaceae         Carex mariposana         750         3600         P-G         CORD           Cyperaceae         Carex nigricans         1900         3700         P-G         CORD           <  | Cyperaceae      |                             | 2600          | 3900          | P-G  | END            |  |  |
| Cyperaceae         Carex filifolia var. erostrata         1500         3700         P-G         CORD           Cyperaceae         Carex haydeniana         2400         4200         P-G         CORD           Cyperaceae         Carex helleri         2400         4100         P-G         S-C           Cyperaceae         Carex heteroneura         1300         4000         P-G         INT           Cyperaceae         Carex hoodii         650         3600         P-G         CORD           Cyperaceae         Carex incurviformis         3700         4000         P-G         CORD           Cyperaceae         Carex jonesii         900         3500         P-G         CORD           Cyperaceae         Carex lenticularis var.         0         3600         P-G         CORD           Cyperaceae         Carex leporinella         1900         4000         P-G         CORD           Cyperaceae         Carex mariposana         750         3600         P-G         CORD           Cyperaceae         Carex milicostata         1900         3500         P-G         CORD           Cyperaceae         Carex nigricans         1900         3700         P-G         CORD <td< td=""><td>Cyperaceae</td><td>Carex deflexa var. boottii</td><td>0</td><td>3800</td><td>P-G</td><td>CORD</td></td<>  | Cyperaceae      | Carex deflexa var. boottii  | 0             | 3800          | P-G  | CORD           |  |  |
| Cyperaceae         Carex haydeniana         2400         4200         P-G         CORD           Cyperaceae         Carex helleri         2400         4100         P-G         S-C           Cyperaceae         Carex heteroneura         1300         4000         P-G         INT           Cyperaceae         Carex hoodii         650         3600         P-G         CORD           Cyperaceae         Carex incurviformis         3700         4000         P-G         CORD           Cyperaceae         Carex jonesii         900         3500         P-G         CORD           Cyperaceae         Carex lenticularis var.         0         3600         P-G         CORD           Cyperaceae         Carex leporinella         1900         4000         P-G         CORD           Cyperaceae         Carex mariposana         750         3600         P-G         CORD           Cyperaceae         Carex multicostata         1900         3500         P-G         CORD           Cyperaceae         Carex migricans         1900         3700         P-G         CORD           Cyperaceae         Carex phaeocephala         2500         4000         P-G         CORD           Cyperaceae  | Cyperaceae      | Carex douglasii             | 300           | 3800          | P-G  | CORD           |  |  |
| Cyperaceae         Carex helleri         2400         4100         P-G         S-C           Cyperaceae         Carex heteroneura         1300         4000         P-G         INT           Cyperaceae         Carex hoodii         650         3600         P-G         CORD           Cyperaceae         Carex incurviformis         3700         4000         P-G         CORD           Cyperaceae         Carex incurviformis         900         3500         P-G         CORD           Cyperaceae         Carex incurviformis         900         3500         P-G         CORD           Cyperaceae         Carex lenticularis var.         0         3600         P-G         CORD           Cyperaceae         Carex leporinella         1900         4000         P-G         CORD           Cyperaceae         Carex mariposana         750         3600         P-G         CORD           Cyperaceae         Carex multicostata         1900         3500         P-G         CORD           Cyperaceae         Carex nigricans         1900         3700         P-G         CORD           Cyperaceae         Carex phaeocephala         2500         4000         P-G         CORD           Cy  | Cyperaceae      |                             | 1500          | 3700          | P-G  | CORD           |  |  |
| Cyperaceae         Carex heteroneura         1300         4000         P-G         INT           Cyperaceae         Carex hoodii         650         3600         P-G         CORD           Cyperaceae         Carex incurviformis         3700         4000         P-G         CORD           Cyperaceae         Carex jonesti         900         3500         P-G         CORD           Cyperaceae         Carex lenticularis var.         0         3600         P-G         CORD           Cyperaceae         Carex leporimella         1900         4000         P-G         CORD           Cyperaceae         Carex mariposana         750         3600         P-G         END-CAL           Cyperaceae         Carex multicostata         1900         3500         P-G         CORD           Cyperaceae         Carex nigricans         1900         3700         P-G         CORD           Cyperaceae         Carex phaeocephala         2500         4000         P-G         CORD           Cyperaceae         Carex proposita         3000         4100         P-G         CORD           Cyperaceae         Carex rossii         0         3800         P-G         CORD           Cyperaceae<  | Cyperaceae      | Carex haydeniana            | 2400          | 4200          | P-G  | CORD           |  |  |
| Cyperaceae         Carex hoodii         650         3600         P-G         CORD           Cyperaceae         Carex incurviformis         3700         4000         P-G         CORD           Cyperaceae         Carex jonesii         900         3500         P-G         CORD           Cyperaceae         Carex lenticularis var.         0         3600         P-G         CORD           Cyperaceae         Carex leporinella         1900         4000         P-G         CORD           Cyperaceae         Carex mariposana         750         3600         P-G         CORD           Cyperaceae         Carex multicostata         1900         3500         P-G         CORD           Cyperaceae         Carex nigricans         1900         3700         P-G         CORD           Cyperaceae         Carex phaeocephala         2500         4000         P-G         CORD           Cyperaceae         Carex proposita         3000         4100         P-G         CORD           Cyperaceae         Carex rossii         0         3800         P-G         CORD           Cyperaceae         Carex spectifica         1200         3500         P-G         CORD           Cy  | Cyperaceae      | Carex helleri               | 2400          | 4100          | P-G  | S-C            |  |  |
| Cyperaceae         Carex incurviformis         3700         4000         P-G         CORD           Cyperaceae         Carex jonesii         900         3500         P-G         CORD           Cyperaceae         Carex lenticularis var.         0         3600         P-G         CORD           Cyperaceae         Carex leporinella         1900         4000         P-G         CORD           Cyperaceae         Carex mariposana         750         3600         P-G         END-CAL           Cyperaceae         Carex multicostata         1900         3500         P-G         CORD           Cyperaceae         Carex nigricans         1900         3700         P-G         CORD           Cyperaceae         Carex phaeocephala         2500         4000         P-G         CORD           Cyperaceae         Carex praeceptorium         2200         3500         P-G         CORD           Cyperaceae         Carex proposita         3000         4100         P-G         CORD           Cyperaceae         Carex scirpoidea var.         2800         3700         P-G         CORD           Cyperaceae         Carex specifica         1200         3500         P-G         CORD   | Cyperaceae      | Carex heteroneura           | 1300          | 4000          | P-G  | INT            |  |  |
| Cyperaceae         Carex jonesii         900         3500         P-G         CORD           Cyperaceae         Carex lenticularis var.         0         3600         P-G         CORD           Lipocarpa           Cyperaceae         Carex leporinella         1900         4000         P-G         CORD           Cyperaceae         Carex mariposana         750         3600         P-G         END-CAL           Cyperaceae         Carex multicostata         1900         3500         P-G         CORD           Cyperaceae         Carex nigricans         1900         3700         P-G         CORD           Cyperaceae         Carex phaeocephala         2500         4000         P-G         CORD           Cyperaceae         Carex praeceptorium         2200         3500         P-G         CORD           Cyperaceae         Carex proposita         3000         4100         P-G         CORD           Cyperaceae         Carex scirpoidea var.         2800         3700         P-G         CORD           Cyperaceae         Carex specifica         1200         3500         P-G         CORD           Cyperaceae         Carex spectabilis         1800         3700 <t< td=""><td>Cyperaceae</td><td>Carex hoodii</td><td>650</td><td>3600</td><td>P-G</td><td>CORD</td></t<>  | Cyperaceae      | Carex hoodii                | 650           | 3600          | P-G  | CORD           |  |  |
| Cyperaceae         Carex lenticularis var.         0         3600         P-G         CORD           Cyperaceae         Carex leporinella         1900         4000         P-G         CORD           Cyperaceae         Carex mariposana         750         3600         P-G         END-CAL           Cyperaceae         Carex multicostata         1900         3500         P-G         CORD           Cyperaceae         Carex nigricans         1900         3700         P-G         CORD           Cyperaceae         Carex phaeocephala         2500         4000         P-G         CORD           Cyperaceae         Carex praeceptorium         2200         3500         P-G         CORD           Cyperaceae         Carex proposita         3000         4100         P-G         S-C           Cyperaceae         Carex sosii         0         3800         P-G         CORD           Cyperaceae         Carex sirpoidea var.         2800         3700         P-G         CORD           Cyperaceae         Carex specifica         1200         3500         P-G         INT           Cyperaceae         Carex specifica         1200         3500         P-G         CORD           Cyp  | Cyperaceae      | Carex incurviformis         | 3700          | 4000          | P-G  | CORD           |  |  |
| Cyperaceae         Carex leporinella         1900         4000         P-G         CORD           Cyperaceae         Carex mariposana         750         3600         P-G         END-CAL           Cyperaceae         Carex multicostata         1900         3500         P-G         CORD           Cyperaceae         Carex nigricans         1900         3700         P-G         CORD           Cyperaceae         Carex phaeocephala         2500         4000         P-G         CORD           Cyperaceae         Carex praeceptorium         2200         3500         P-G         CORD           Cyperaceae         Carex proposita         3000         4100         P-G         S-C           Cyperaceae         Carex rossii         0         3800         P-G         CORD           Cyperaceae         Carex sirpoidea var.         2800         3700         P-G         CORD           Cyperaceae         Carex specifica         1200         3500         P-G         INT           Cyperaceae         Carex specifica         1200         3500         P-G         CORD           Cyperaceae         Carex straminiformis         1700         4100         P-G         S-C           Cyp  | Cyperaceae      | Carex jonesii               | 900           |               | P-G  |                |  |  |
| Cyperaceae         Carex mariposana         750         3600         P-G         END-CAL           Cyperaceae         Carex multicostata         1900         3500         P-G         CORD           Cyperaceae         Carex nigricans         1900         3700         P-G         CORD           Cyperaceae         Carex phaeocephala         2500         4000         P-G         CORD           Cyperaceae         Carex praeceptorium         2200         3500         P-G         CORD           Cyperaceae         Carex proposita         3000         4100         P-G         S-C           Cyperaceae         Carex scripoidea var.         2800         3700         P-G         CORD           Cyperaceae         Carex specifica         1200         3500         P-G         INT           Cyperaceae         Carex specifica         1200         3500         P-G         CORD           Cyperaceae         Carex specifica         1800         3700         P-G         CORD           Cyperaceae         Carex straminiformis         1700         4100         P-G         S-C           Cyperaceae         Carex subfusca         700         3800         P-G         INT           C  | Cyperaceae      |                             | 0             | 3600          | P-G  | CORD           |  |  |
| Cyperaceae         Carex multicostata         1900         3500         P-G         CORD           Cyperaceae         Carex nigricans         1900         3700         P-G         CORD           Cyperaceae         Carex phaeocephala         2500         4000         P-G         CORD           Cyperaceae         Carex praeceptorium         2200         3500         P-G         CORD           Cyperaceae         Carex proposita         3000         4100         P-G         S-C           Cyperaceae         Carex sossii         0         3800         P-G         CORD           Cyperaceae         Carex scirpoidea var.         2800         3700         P-G         CORD           Cyperaceae         Carex specifica         1200         3500         P-G         INT           Cyperaceae         Carex specifica         1800         3700         P-G         CORD           Cyperaceae         Carex specifica         1800         3700         P-G         CORD           Cyperaceae         Carex straminiformis         1700         4100         P-G         S-C           Cyperaceae         Carex subfusca         700         3800         P-G         INT           Cyperaceae  |                 | Carex leporinella           | 1900          | 4000          | P-G  | CORD           |  |  |
| Cyperaceae         Carex nigricans         1900         3700         P-G         CORD           Cyperaceae         Carex phaeocephala         2500         4000         P-G         CORD           Cyperaceae         Carex praeceptorium         2200         3500         P-G         CORD           Cyperaceae         Carex proposita         3000         4100         P-G         S-C           Cyperaceae         Carex sossii         0         3800         P-G         CORD           Cyperaceae         Carex scirpoidea var.         2800         3700         P-G         CORD           Cyperaceae         Carex specifica         1200         3500         P-G         INT           Cyperaceae         Carex specifica         1800         3700         P-G         CORD           Cyperaceae         Carex spectabilis         1800         3700         P-G         CORD           Cyperaceae         Carex straminiformis         1700         4100         P-G         S-C           Cyperaceae         Carex subfusca         700         3800         P-G         INT           Cyperaceae         Carex subnigricans         2600         3800         P-G         CORD   |                 | Carex mariposana            |               | 3600          | P-G  | <b>END-CAL</b> |  |  |
| Cyperaceae         Carex phaeocephala         2500         4000         P-G         CORD           Cyperaceae         Carex praeceptorium         2200         3500         P-G         CORD           Cyperaceae         Carex proposita         3000         4100         P-G         S-C           Cyperaceae         Carex rossii         0         3800         P-G         CORD           Cyperaceae         Carex scirpoidea var.         2800         3700         P-G         CORD           Cyperaceae         Carex specifica         1200         3500         P-G         INT           Cyperaceae         Carex spectabilis         1800         3700         P-G         CORD           Cyperaceae         Carex straminiformis         1700         4100         P-G         S-C           Cyperaceae         Carex subfusca         700         3800         P-G         INT           Cyperaceae         Carex subnigricans         2600         3800         P-G         CORD   | Cyperaceae      | Carex multicostata          | 1900          | 3500          | P-G  | CORD           |  |  |
| Cyperaceae         Carex praeceptorium         2200         3500         P-G         CORD           Cyperaceae         Carex proposita         3000         4100         P-G         S-C           Cyperaceae         Carex rossii         0         3800         P-G         CORD           Cyperaceae         Carex scirpoidea var.         2800         3700         P-G         CORD           Seudoscirpoidea           Cyperaceae         Carex specifica         1200         3500         P-G         INT           Cyperaceae         Carex spectabilis         1800         3700         P-G         CORD           Cyperaceae         Carex straminiformis         1700         4100         P-G         S-C           Cyperaceae         Carex subfusca         700         3800         P-G         INT           Cyperaceae         Carex subnigricans         2600         3800         P-G         CORD  | Cyperaceae      | Carex nigricans             | 1900          | 3700          | P-G  |                |  |  |
| Cyperaceae         Carex proposita         3000         4100         P-G         S-C           Cyperaceae         Carex rossii         0         3800         P-G         CORD           Cyperaceae         Carex scirpoidea var.         2800         3700         P-G         CORD           Seudoscirpoidea           Cyperaceae         Carex specifica         1200         3500         P-G         INT           Cyperaceae         Carex spectabilis         1800         3700         P-G         CORD           Cyperaceae         Carex straminiformis         1700         4100         P-G         S-C           Cyperaceae         Carex subfusca         700         3800         P-G         INT           Cyperaceae         Carex subnigricans         2600         3800         P-G         CORD  | Cyperaceae      | Carex phaeocephala          | 2500          | 4000          | P-G  |                |  |  |
| Cyperaceae         Carex rossii         0         3800         P-G         CORD           Cyperaceae         Carex scirpoidea var.         2800         3700         P-G         CORD           pseudoscirpoidea           Cyperaceae         Carex specifica         1200         3500         P-G         INT           Cyperaceae         Carex spectabilis         1800         3700         P-G         CORD           Cyperaceae         Carex straminiformis         1700         4100         P-G         S-C           Cyperaceae         Carex subfusca         700         3800         P-G         INT           Cyperaceae         Carex subnigricans         2600         3800         P-G         CORD  | Cyperaceae      | Carex praeceptorium         | 2200          | 3500          | P-G  | CORD           |  |  |
| Cyperaceae         Carex scirpoidea var. pseudoscirpoidea         2800         3700         P-G         CORD           Cyperaceae         Carex specifica         1200         3500         P-G         INT           Cyperaceae         Carex speciabilis         1800         3700         P-G         CORD           Cyperaceae         Carex straminiformis         1700         4100         P-G         S-C           Cyperaceae         Carex subfusca         700         3800         P-G         INT           Cyperaceae         Carex subnigricans         2600         3800         P-G         CORD  | Cyperaceae      | Carex proposita             | 3000          |               | P-G  |                |  |  |
| pseudoscirpoideaCyperaceaeCarex specifica12003500P-GINTCyperaceaeCarex spectabilis18003700P-GCORDCyperaceaeCarex straminiformis17004100P-GS-CCyperaceaeCarex subfusca7003800P-GINTCyperaceaeCarex subnigricans26003800P-GCORD  |                 | Carex rossii                |               |               |      | CORD           |  |  |
| CyperaceaeCarex specifica12003500P-GINTCyperaceaeCarex spectabilis18003700P-GCORDCyperaceaeCarex straminiformis17004100P-GS-CCyperaceaeCarex subfusca7003800P-GINTCyperaceaeCarex subnigricans26003800P-GCORD  | Cyperaceae      |                             | 2800          | 3700          | P-G  | CORD           |  |  |
| CyperaceaeCarex spectabilis18003700P-GCORDCyperaceaeCarex straminiformis17004100P-GS-CCyperaceaeCarex subfusca7003800P-GINTCyperaceaeCarex subnigricans26003800P-GCORD   | C               |                             | 1000          | 2.500         | D ~  | TA IOT         |  |  |
| CyperaceaeCarex straminiformis17004100P-GS-CCyperaceaeCarex subfusca7003800P-GINTCyperaceaeCarex subnigricans26003800P-GCORD   |                 |                             |               |               |      |                |  |  |
| CyperaceaeCarex subfusca7003800P-GINTCyperaceaeCarex subnigricans26003800P-GCORD   | - A             |                             |               |               |      |                |  |  |
| Cyperaceae Carex subnigricans 2600 3800 P-G CORD   |                 |                             |               |               |      |                |  |  |
|  |                 |                             |               |               |      |                |  |  |
| Cyperaceae Carex tahoensis 3200 3700 P-G CORD  |                 |                             |               |               |      |                |  |  |
|  | Cyperaceae      | Carex tahoensis             | 3200          | 3/00          | P-G  | CORD           |  |  |

| APPENDIX 1. CONTINUED. |                                      |               |               |            |               |  |  |
|------------------------|--------------------------------------|---------------|---------------|------------|---------------|--|--|
|                        | Specific or                          | Lower         | Upper         | Growth     | Biogeographic |  |  |
| Higher level taxor     |                                      | elevation (m) | elevation (m) | form       | relationship  |  |  |
| Cyperaceae             | Carex vernacula                      | 1800          | 4000          | P-G        | CORD          |  |  |
| Cyperaceae             | Eleocharis quinqueflora              | 40            | 3600          | P-G        | WIDE          |  |  |
| Cyperaceae             | Trichophorum clementis               | 2400          | 3600          | P-G        | END           |  |  |
| Juncaceae              | Juncus bryoides                      | 600           | 3600          | P-G        | CORD          |  |  |
|                        | 2                                    | 200           | 3500          | P-G        | CORD          |  |  |
| Juncaceae              | Juncus drummondii                    | 1200          | 3500          | P-G        | CORD          |  |  |
| Juncaceae              | Juncus mertensianus                  |               |               |            |               |  |  |
| Juncaceae              | Juncus mexicanus                     | 0             | 3800          | P-G        | WIDE          |  |  |
| Juncaceae              | Juncus orthophyllus                  | 1200          | 3500          | P-G        | CORD          |  |  |
| Juncaceae              | Juncus parryi                        | 2000          | 3800          | P-G        | CORD          |  |  |
| Juncaceae              | Luzula divaricata                    | 2100          | 3700          | P-G        | S-C           |  |  |
| Juncaceae              | Luzula orestera                      | 2700          | 3600          | P-G        | END           |  |  |
| Juncaceae              | Luzula spicata                       | 2900          | 3700          | P-G        | WIDE          |  |  |
| Juncaceae              | Luzula subcongesta                   | 2000          | 3500          | P-G        | S-C           |  |  |
| Juncaginaceae          | Triglochin palustris                 | 2400          | 3500          | P-G        | WIDE          |  |  |
| Liliaceae              | Calochortus leichtlinii              | 1300          | 4000          | G          | S-C           |  |  |
| Melanthiaceae          | Veratrum californicum var.           | 0             | 3500          | G          | CORD          |  |  |
|                        | californicum                         |               |               |            |               |  |  |
| Poaceae                | Agrostis idahoensis                  | 0             | 3500          | P-G        | CORD          |  |  |
| Poaceae                | Agrostis pallens                     | 200           | 3500          | P-G        | CORD          |  |  |
| Poaceae                | Agrostis scabra                      | 100           | 3500          | P-G        | WIDE          |  |  |
| Poaceae                | Agrostis thurberiana                 | 1300          | 3500          | P-G        | CORD          |  |  |
| Poaceae                | Agrostis variabilis                  | 1600          | 4000          | P-G        | CORD          |  |  |
| Poaceae                | Alopecurus aequalis var              | 50            | 3500          | P-G        | WIDE          |  |  |
| Toaccac                | aequalis                             | 30            | 3300          | 1-0        | WIDE          |  |  |
| Poaceae                | Bromus carinatus var.                | 0             | 3500          | P-G        | S-C           |  |  |
| roaceae                |                                      | U             | 3300          | r-G        | 3-C           |  |  |
| D                      | carinatus                            | 0             | 2500          | D.C        | 0.0           |  |  |
| Poaceae                | Bromus carinatus var.                | 0             | 3500          | P-G        | S-C           |  |  |
| _                      | marginatus                           | <b>.</b>      | ****          | T. C       | ~ ~           |  |  |
| Poaceae                | Bromus orcuttianus                   | 560           | 3500          | P-G        | S-C           |  |  |
| Poaceae                | Bromus porteri                       | 550           | 3500          | P-G        | CORD          |  |  |
| Poaceae                | Bromus richardsonii                  | 1200          | 3600          | P-G        | CORD          |  |  |
| Poaceae                | Calamagrostis muiriana               | 2480          | 3900          | P-G        | END           |  |  |
| Poaceae                | Calamagrostis purpurascens           | 1300          | 4000          | P-G        | WIDE          |  |  |
| Poaceae                | Deschampsia cespitosa                | 0             | 3820          | P-G        | WIDE          |  |  |
|                        | subsp. <i>cespitosa</i>              |               |               |            |               |  |  |
| Poaceae                | Elymus elymoides subsp.              | 275           | 4200          | P-G        | CORD          |  |  |
|                        | californicus                         |               |               |            |               |  |  |
| Poaceae                | Elymus multisetus                    | 0             | 3800          | P-G        | CORD          |  |  |
| Poaceae                | Elymus scribneri                     | 2900          | 4200          | P-G        | CORD          |  |  |
| Poaceae                | Elymus sierrae                       | 1800          | 3530          | P-G        | INT           |  |  |
| Poaceae                | Festuca brachyphylla subsp.          | 2800          | 4300          | P-G        | WIDE          |  |  |
| Touceac                | breviculmis                          | 2000          | 1500          | . 0        | WIDE          |  |  |
| Poaceae                | Festuca minutiflora                  | 2850          | 4050          | P-G        | CORD          |  |  |
| Poaceae                | Hordeum jubatum var.                 | 20            | 3500          | P-G        | WIDE          |  |  |
| roaceae                | 3                                    | 20            | 3300          | 1-0        | WIDE          |  |  |
| Danasaa                | jubatum<br>Ka alawi a sa a sa sa tha | 0             | 3840          | P-G        | WIDE          |  |  |
| Poaceae                | Koeleria macrantha                   |               |               | P-G        |               |  |  |
| Poaceae                | Muhlenbergia richardsonis            | 1220          | 3670          |            | CORD          |  |  |
| Poaceae                | Phleum alpinum                       | 0             | 3700          | P-G        | WIDE          |  |  |
| Poaceae                | Poa abbreviata subsp.                | 3300          | 3660          | P-G        | CORD          |  |  |
| _                      | pattersonii                          |               | 2.000         | <b>5</b> C | CORD          |  |  |
| Poaceae                | Poa cusickii subsp. epilis           | 2400          | 3600          | P-G        | CORD          |  |  |
| Poaceae                | Poa cusickii subsp.                  | 2100          | 3500          | P-G        | S-C           |  |  |
|                        | purpurascens                         |               |               |            |               |  |  |
| Poaceae                | Poa glauca subsp. rupicola           | 3300          | 4100          | P-G        | CORD          |  |  |
| Poaceae                | Poa keckii                           | 3300          | 4340          | P-G        | END-CAL       |  |  |
| Poaceae                | Poa lettermanii                      | 3500          | 4300          | P-G        | CORD          |  |  |
| Poaceae                | Poa secunda subsp. secunda           | 0             | 3900          | P-G        | CORD          |  |  |
| Poaceae                | Poa stebbinsii                       | 2700          | 3700          | P-G        | END           |  |  |
| Poaceae                | Poa wheeleri                         | 1300          | 3800          | P-G        | CORD          |  |  |
| Poaceae                | Stipa hymenoides                     | 60            | 3500          | P-G        | CORD          |  |  |
| Poaceae                | Stipa kingii                         | 2000          | 3650          | P-G        | END           |  |  |
| Poaceae                | Stipa nelsonii subsp. dorei          | 450           | 3500          | P-G        | CORD          |  |  |
| Poaceae                | Stipa occidentalis subsp.            | 1200          | 3500          | P-G        | CORD          |  |  |
| 1 Oaccac               | pubescens                            | 1200          | 3300          | 1-0        | CORD          |  |  |
|                        | puvescens                            |               |               |            |               |  |  |

| APPENDIX I. CONTINUED. |  |                     |                     |             |                            |  |  |
|------------------------|--|---------------------|---------------------|-------------|----------------------------|--|--|
| Higher level taxon     | Specific or infraspecific taxon                | Lower elevation (m) | Upper elevation (m) | Growth form | Biogeographic relationship |  |  |
| Poaceae                | Stipa pinetorum                                | 2000                | 3900                | P-G         | INT                        |  |  |
| Poaceae                | Stipa webberi                                  | 1450                | 3500                | P-G         | INT                        |  |  |
| Poaceae                | Torreyochloa erecta                            | 2000                | 3500                | P-G         | INT                        |  |  |
| Poaceae                | Torreyochloa pallida var. pauciflora           | 0                   | 3500                | P-G         | CORD                       |  |  |
| Poaceae<br>Themidaceae | Trisetum spicatum<br>Triteleia dudleyi         | 1370<br>1200        | 3900<br>3500        | P-G<br>G    | WIDE<br>END-CAL            |  |  |
| EUDICOTS               |  |                     |                     |             |                            |  |  |
| Adoxaceae              | Sambucus racemosa var.<br>melanocarpa          | 1800                | 3600                | S           | CORD                       |  |  |
| Apiaceae               | Cymopterus cinerarius                          | 2100                | 3500                | P           | INT                        |  |  |
| Apiaceae               | Oreonana clementis                             | 1500                | 4000                | P           | END                        |  |  |
| Apiaceae               | Podistera nevadensis                           | 3000                | 4000                | P           | INT                        |  |  |
| Apiaceae               | Sphenosciadium capitellatum                    | 0                   | 3500                | P           | CORD                       |  |  |
| Asteraceae             | Achillea millefolium                           | 0                   | 3650                | P           | WIDE                       |  |  |
| Asteraceae             | Ageratina occidentalis                         | 0                   | 3700                | P           | CORD                       |  |  |
| Asteraceae             | Agoseris aurantiaca var.<br>aurantiaca         | 1500                | 3500                | P           | CORD                       |  |  |
| Asteraceae             | Agoseris monticola                             | 2500                | 3800                | P           | S-C                        |  |  |
| Asteraceae             | Antennaria media                               | 1800                | 3900                | P-MAT       | CORD                       |  |  |
| Asteraceae             | Antennaria pulchella                           | 2800                | 3700                | P-MAT       | INT                        |  |  |
| Asteraceae             | Antennaria rosea subsp. confinis               | 1200                | 3700                | P           | WIDE                       |  |  |
| Asteraceae             | Antennaria rosea subsp. rosea                  | 1200                | 3700                | P-MAT       | CORD                       |  |  |
| Asteraceae             | Antennaria umbrinella                          | 1800                | 3900                | P-MAT       | WIDE                       |  |  |
| Asteraceae             | Arnica chamissonis                             | 1800                | 3500                | P           | WIDE                       |  |  |
| Asteraceae             | Arnica lanceolata subsp. prima                 | 2200                | 3500                | P           | CORD                       |  |  |
| Asteraceae             | Arnica longifolia                              | 1300                | 3500                | P           | CORD                       |  |  |
| Asteraceae             | Arnica mollis                                  | 2500                | 3500                | P           | CORD                       |  |  |
| Asteraceae             | Arnica ovata                                   | 1800                | 3600                | P           | CORD                       |  |  |
| Asteraceae             | Artemisia arbuscula subsp. arbuscula           | 1500                | 3800                | S           | CORD                       |  |  |
| Asteraceae             | Artemisia ludoviciana subsp. incompta          | 0                   | 3500                | P           | INT                        |  |  |
| Asteraceae             | Artemisia norvegica subsp. saxatilis           | 2300                | 3800                | P           | WIDE                       |  |  |
| Asteraceae             | Artemisia spiciformis                          | 2100                | 3700                | P           | CORD                       |  |  |
| Asteraceae             | Chaenactis alpigena                            | 220                 | 3900                | P-MAT       | END-CAL                    |  |  |
| Asteraceae             | Chaenactis douglasii var.<br>douglasii         | 400                 | 3500                | Р           | CORD                       |  |  |
| Asteraceae             | Chrysothamnus viscidiflorus var. viscidiflorus | 900                 | 4000                | SS          | INT                        |  |  |
| Asteraceae             | Cirsium arizonicum var.<br>arizonicum          | 2300                | 3500                | Р           | INT                        |  |  |
| Asteraceae             | Cirsium occidentale var. venustum              | 0                   | 3600                | P           | INT                        |  |  |
| Asteraceae             | Cirsium scariosum var.<br>americanum           | 1600                | 3500                | P           | CORD                       |  |  |
| Asteraceae             | Crepis nana                                    | 2000                | 4000                | P-MAT       | CORD                       |  |  |
| Asteraceae             | Ericameria bloomeri                            | 900                 | 4000                | SS          | INT                        |  |  |
| Asteraceae             | Ericameria discoidea                           | 2300                | 3800                | SS          | INT                        |  |  |
| Asteraceae             | Ericameria nauseosa var. speciosa              | 50                  | 3500                | S           | INT                        |  |  |
| Asteraceae             | Ericameria parryi var.<br>monocephala          | 2800                | 3700                | SS          | INT                        |  |  |
| Asteraceae             | Ericameria suffruticosa                        | 2100                | 3800                | SS          | INT                        |  |  |
| Asteraceae             | Erigeron algidus                               | 2600                | 3700                | P           | INT                        |  |  |
| Asteraceae             | Erigeron compositus                            | 2000                | 4300                | P-MAT       | WIDE                       |  |  |
| Asteraceae             | Erigeron lonchophyllus                         | 1800                | 3550                | P-A         | WIDE                       |  |  |
| Asteraceae             | Erigeron pygmaeus                              | 2900                | 4100                | P-MAT       | S-C                        |  |  |
| Asteraceae             | Erigeron vagus                                 | 3300                | 4400                | P-MAT       | INT                        |  |  |
|                        |  |                     |                     |             |                            |  |  |

|                              | Appendix 1. Continued.                    |                     |                     |             |                            |  |  |
|------------------------------|---|---------------------|---------------------|-------------|----------------------------|--|--|
| Higher level taxon           | Specific or infraspecific taxon           | Lower elevation (m) | Upper elevation (m) | Growth form | Biogeographic relationship |  |  |
| Asteraceae                   | Eriophyllum lanatum var. integrifolium    | 1400                | 3500                | P           | CORD                       |  |  |
| Asteraceae                   | Hazardia whitneyi var.<br>whitneyi        | 1200                | 3500                | SS          | END                        |  |  |
| Asteraceae                   | Hieracium nudicaule                       | 1800                | 3500                | P           | S-C                        |  |  |
| Asteraceae                   | Hieracium triste                          | 1650                | 3550                | P           | CORD                       |  |  |
| Asteraceae                   | Hulsea algida                             | 3000                | 4000                | P           | INT                        |  |  |
| Asteraceae                   | Hulsea vestita subsp. pygmaea             | 3200                | 3900                | P           | END-CAL                    |  |  |
| Asteraceae                   | Hymenoxys hoopesii                        | 1500                | 3650                | P           | CORD                       |  |  |
| Asteraceae                   | Oreostemma alpigenum var. andersonii      | 1200                | 3500                | P           | S-C                        |  |  |
| Asteraceae                   | Oreostemma peirsonii                      | 3000                | 3800                | P           | END                        |  |  |
| Asteraceae                   | Orochaenactis<br>thysanocarpha            | 1600                | 3800                | A           | END                        |  |  |
| Asteraceae                   | Packera cana                              | 1200                | 3500                | P           | S-C                        |  |  |
| Asteraceae                   | Packera werneriifolia                     | 3000                | 3650                | P           | S-C                        |  |  |
| Asteraceae                   | Pyrrocoma apargioides                     | 2200                | 3800                | P           | S-C                        |  |  |
| Asteraceae                   | Raillardella argentea                     | 1800                | 3900                | P           | S-C                        |  |  |
| Asteraceae                   | Raillardella scaposa                      | 2000                | 3500                | P           | S-C                        |  |  |
| Asteraceae                   | Senecio fremontii var.                    | 2800                | 4000                | P-MAT       | S-C                        |  |  |
| Asteraceae                   | Senecio integerrimus var.<br>major        | 100                 | 3600                | P           | CORD                       |  |  |
| Asteraceae                   | Senecio pattersonensis                    | 3000                | 3700                | P           | INT                        |  |  |
| Asteraceae                   | Senecio scorzonella                       | 1600                | 3500                | P           | S-C                        |  |  |
| Asteraceae                   | Senecio spartioides                       | 1000                | 3500                | SS          | CORD                       |  |  |
| Asteraceae                   | Solidago multiradiata                     | 1250                | 3950                | P           | CORD                       |  |  |
| Asteraceae                   | Sphaeromeria cana                         | 1800                | 4000                | SS          | CORD                       |  |  |
| Asteraceae                   | Stenotis acaulis                          | 1800                | 3600                | P-MAT       | INT                        |  |  |
| Asteraceae                   | Tonestus peirsonii                        | 2900                | 3700                | P           | <b>END-CAL</b>             |  |  |
| Boraginaceae                 | Cryptantha circumscissa var. circumscissa | 150                 | 3650                | A           | CORD                       |  |  |
| Boraginaceae                 | Cryptantha circumscissa var. rosulata     | 2950                | 3650                | A           | END                        |  |  |
| Boraginaceae                 | Cryptantha glomeriflora                   | 1800                | 3750                | Α           | S-C                        |  |  |
| Boraginaceae                 | Cryptantha humilis                        | 1700                | 3600                | P           | INT                        |  |  |
| Boraginaceae                 | Cryptantha nubigena                       | 2400                | 3900                | P           | INT                        |  |  |
| Boraginaceae                 | Hackelia micrantha                        | 1200                | 3500                | P           | CORD                       |  |  |
| Boraginaceae                 | Hackelia sharsmithii                      | 3150                | 3700                | P           | INT                        |  |  |
| Boraginaceae                 | Nama densum                               | 880                 | 3560                | Α           | INT                        |  |  |
| Boraginaceae                 | Phacelia hastata subsp. compacta          | 1500                | 4000                | Α           | S-C                        |  |  |
| Boraginaceae                 | Phacelia mutabilis                        | 900                 | 3500                | P           | S-C                        |  |  |
| Boraginaceae                 | Phacelia ramosissima                      | 0                   | 3800                | P           | CORD                       |  |  |
| Brassicaceae                 | Anelsonia eurycarpa                       | 1600                | 4100                | P-MAT       | S-C                        |  |  |
| Brassicaceae                 | Boechera depauperata                      | 3650                | 3900                | P           | INT                        |  |  |
| Brassicaceae                 | Boechera howellii                         | 1500                | 3800                | P           | S-C                        |  |  |
| Brassicaceae                 | Boechera inyoensis                        | 1200                | 3500                | P           | INT                        |  |  |
| Brassicaceae                 | Boechera covillei                         | 2200                | 3500                | P           | S-C                        |  |  |
| Brassicaceae                 | Boechera inyoensis                        | 1200                | 3500                | P           | INT                        |  |  |
| Brassicaceae                 | Boechera lemmonii                         | 2000                | 4350                | P           | INT                        |  |  |
| Brassicaceae                 | Boechera lyallii                          | 2000                | 3900                | P           | CORD                       |  |  |
| Brassicaceae                 | Boechera paupercula                       | 2500                | 3700                | P           | CORD                       |  |  |
| Brassicaceae                 | Boechera repanda                          | 1400                | 3600                | P           | INT                        |  |  |
| Brassicaceae                 | Boechera tiehmii                          | 3000                | 3600                | P           | INT                        |  |  |
| Brassicaceae                 | Cardamine cordifolia                      | 600                 | 3600                | P           | CORD                       |  |  |
| Brassicaceae                 | Descurainia incana                        | 100                 | 3500                | P           | CORD                       |  |  |
| Brassicaceae                 | Draba albertina                           | 900                 | 3700                | P-A         | CORD                       |  |  |
| Brassicaceae                 | Draba breweri                             | 3100                | 4100                | P<br>P      | END-CAL                    |  |  |
| Brassicaceae                 | Draba cana                                | 0<br>2500           | 4100                | P<br>P      | CORD<br>END                |  |  |
| Brassicaceae<br>Brassicaceae | Draba cruciata<br>Draba densifolia        | 1900                | 3963<br>3650        | P-MAT       | INT                        |  |  |
| Brassicaceae                 | Draba lemmonii                            | 3050                | 4000                | P           | END                        |  |  |

| Appendix 1. Continued.    |   |               |               |                    |               |  |
|---------------------------|---|---------------|---------------|--------------------|---------------|--|
|                           | Specific or                             | Lower         | Upper         | Growth             | Biogeographic |  |
| Higher level taxon        | infraspecific taxon                     | elevation (m) | elevation (m) | form               | relationship  |  |
| Brassicaceae              | Draba lonchocarpa                       | 2800          | 4000          | P                  | WIDE          |  |
| Brassicaceae              | Draba longisquamosa                     | 3000          | 3900          | P                  | END           |  |
| Brassicaceae              | Draba novolympica                       | 1500          | 3700          | P-MAT              | CORD          |  |
| Brassicaceae              | Draba oligosperma                       | 2000          | 3900          | P-MAT              | CORD          |  |
| Brassicaceae              | Draba praealta<br>Draba sharsmithii     | 2500<br>3300  | 4100<br>3800  | P<br>P             | WIDE<br>END   |  |
| Brassicaceae Brassicaceae | Draba sierrae                           | 3500          | 4114          | P-MAT              | END           |  |
| Brassicaceae              | Draba subumbellata                      | 3300          | 4100          | P-MAT              | END-CAL       |  |
| Brassicaceae              | Erysimum capitatum var.                 | 0             | 4000          | P                  | WIDE          |  |
| <b>Diagonal</b>           | capitatum                               |               |               |                    |               |  |
| Brassicaceae              | Erysimum perenne                        | 2000          | 4000          | P                  | S-C           |  |
| Brassicaceae              | Lepidium densiflorum                    | 0             | 3500          | P-A                | WIDE          |  |
| Brassicaceae              | Rorippa curvipes                        | 100           | 3500          | P-A                | CORD          |  |
| Brassicaceae              | Rorippa curvisiliqua                    | 0             | 3500          | A                  | CORD          |  |
| Brassicaceae              | Streptanthus gracilis                   | 2600          | 3600          | A                  | END           |  |
| Brassicaceae              | Streptanthus tortuosus                  | 200           | 4100          | P                  | S-C           |  |
| Caryophyllaceae           | Cerastium beeringianum                  | 2900          | 4300          | P-MAT              | WIDE          |  |
| Caryophyllaceae           | Ereomogone kingii var.<br>glabrescens   | 2100          | 4050          | P-MAT              | S-C           |  |
| Caryophyllaceae           | Minuartia nuttallii var.                | 2600          | 3800          | P-MAT              | S-C           |  |
| Caryophynaceae            | gracilis                                | 2000          | 3800          | 1 -1/1/4 1         | 5-C           |  |
| Caryophyllaceae           | Minuartia obtusiloba                    | 3150          | 3700          | P-MAT              | CORD          |  |
| Caryophyllaceae           | Minuartia rubella                       | 2400          | 3800          | P                  | CORD          |  |
| Caryophyllaceae           | Minuartia stricta                       | 3500          | 3900          | P                  | CORD          |  |
| Caryophyllaceae           | Sagina saginoides                       | 1000          | 3800          | P                  | WIDE          |  |
| Caryophyllaceae           | Silene bernardina                       | 1350          | 3600          | P                  | CORD          |  |
| Caryophyllaceae           | Silene sargentii                        | 2400          | 3800          | P                  | S-C           |  |
| Caryophyllaceae           | Stellaria calycantha                    | 1700          | 3800          | P                  | WIDE          |  |
| Chenopodiaceae            | Chenopodium atrovirens                  | 300           | 3500          | A                  | CORD          |  |
| Chenopodiaceae            | Monolepis nuttalliana                   | 0             | 3700          | A                  | CORD          |  |
| Crassulaceae              | Rhodiola integrifolia                   | 1800          | 4000          | P                  | WIDE          |  |
| Crassulaceae              | Sedum obtusatum subsp.                  | 1200          | 3700          | P                  | S-C           |  |
| Ericaceae                 | obtusatum<br>Cassiope mertensiana       | 1800          | 3505          | S                  | CORD          |  |
| Ericaceae                 | Gaultheria humifusa                     | 1350          | 4000          | S                  | CORD          |  |
| Ericaceae                 | Kalmia polifolia subsp.                 | 1000          | 3500          | Š                  | CORD          |  |
| Liteaceae                 | microphylla                             | 1000          | 3300          | 5                  | CORD          |  |
| Ericaceae                 | Phyllodoce breweri                      | 1200          | 3500          | S                  | END-CAL       |  |
| Ericaceae                 | Pterospora andromedea                   | 60            | 3700          | P                  | WIDE          |  |
| Ericaceae                 | Rhododendron columbianum                | 0             | 3630          | S                  | CORD          |  |
| Fabaceae                  | Astragalus kentrophyta var.             | 2900          | 4000          | P-MAT              | END-CAL       |  |
|                           | danaus                                  |               |               |                    |               |  |
| Fabaceae                  | Astragalus kentrophyta var.             | 2700          | 3600          | P                  | CORD          |  |
| F 1                       | tegetarius                              |               |               | _                  |               |  |
| Fabaceae                  | Astragalus lentiginosus var.            | 1250          | 3700          | P                  | INT           |  |
| Echococc                  | ineptus                                 | 2250          | 2500          | D                  | INIT          |  |
| Fabaceae<br>Fabaceae      | Astragalus platytropus                  | 2350<br>1500  | 3500<br>3650  | P<br>P             | INT<br>INT    |  |
| rabaceae                  | Astragalus purshii var.<br>lectulus     | 1500          | 3030          | Р                  | 11N 1         |  |
| Fabaceae                  | Astragalus whitneyi var.                | 1550          | 3500          | P                  | S-C           |  |
| rubuccuc                  | whitneyi                                | 1330          | 3300          |                    | 5.6           |  |
| Fabaceae                  | Lupinus adsurgens                       | 1000          | 3500          | P                  | S-C           |  |
| Fabaceae                  | Lupinus angustiflorus                   | 1000          | 3500          | $\hat{\mathbf{P}}$ | INT           |  |
| Fabaceae                  | Lupinus argenteus var.                  | 1500          | 3500          | P                  | INT           |  |
|                           | meionanthus                             |               |               |                    |               |  |
| Fabaceae                  | Lupinus argenteus var.                  | 2500          | 3500          | P                  | INT           |  |
|                           | montigenus                              |               |               |                    |               |  |
| Fabaceae                  | Lupinus breweri var. breweri            | 1000          | 4000          | P-MAT              | END-CAL       |  |
| Fabaceae                  | Lupinus breweri var.                    | 2500          | 4000          | P-MAT              | END-CAL       |  |
| Fohoa                     | bryoides                                | 2000          | 2500          | D 1445             | TATE          |  |
| Fabaceae                  | Lupinus breweri var.                    | 2000          | 3500          | P-MAT              | INT           |  |
| Fabaceae                  | grandiflorus                            | 2500          | 3500          | P                  | END           |  |
| Fabaceae                  | Lupinus covillei<br>Lupinus gracilentus | 2500<br>2500  | 3500          | P<br>P             | END           |  |
|                           | zopuno gracuentas                       | 2500          | 5500          |                    |               |  |

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|--------------------|---|---------------------|---------------------|-------------|----------------------------|
| Higher level taxon | Specific or infraspecific taxon                 | Lower elevation (m) | Upper elevation (m) | Growth form | Biogeographic relationship |
| Fabaceae           | Lupinus latifolius var.<br>columbianus          | 1000                | 3500                | P           | S-C                        |
| Fabaceae           | Lupinus latifolius var. parishii                | 0                   | 3500                | P           | END-CAL                    |
| Fabaceae           | Lupinus lepidus var. lobbii                     | 2000                | 3500                | P           | S-C                        |
| Fabaceae           | Lupinus lepidus var. ramosus                    | 3000                | 4000                | P           | END-CAL                    |
| Fabaceae           | Lupinus obtusilobus                             | 2500                | 3500                | P           | S-C                        |
| Fabaceae           | Lupinus padre-crowleyi                          | 2500                | 4000                | P-MAT       | END-CAL                    |
| Fabaceae           | Lupinus pratensis var. pratensis                | 1000                | 3500                | P           | END-CAL                    |
| Fabaceae           | Oxytropis borealis var.                         | 3300                | 3900                | P           | INT                        |
| Fabaceae           | Oxytropis borealis var.                         | 3300                | 3900                | P           | CORD                       |
| Fabaceae           | Oxytropis parryi                                | 3100                | 3800                | P-MAT       | INT                        |
| Fabaceae           | Trifolium kingii subsp.                         | 2100                | 3500                | P           | END                        |
| Fabaceae           | dedeckerae Trifolium monanthum subsp. monanthum | 1700                | 3900                | P-MAT       | INT                        |
| Gentianaceae       | Comastoma tenellum                              | 3200                | 3900                | Α           | WIDE                       |
| Gentianaceae       | Gentiana calycosa                               | 1300                | 3900                | P           | CORD                       |
| Gentianaceae       | Gentiana newberryi var.<br>tiogana              | 1500                | 4000                | P           | S-C                        |
| Gentianaceae       | Gentianella amarella subsp.                     | 1500                | 3500                | A           | WIDE                       |
| Gentianaceae       | Gentianopsis holopetala                         | 1800                | 4000                | A           | S-C                        |
| Grossulariaceae    | Ribes cereum var. inebrians                     | 2100                | 3850                | S           | INT                        |
| Grossulariaceae    | Ribes montigenum                                | 800                 | 4000                | Š           | CORD                       |
| Grossulariaceae    | Ribes velutinum                                 | 700                 | 3500                | Š           | CORD                       |
| Hydrangeaceae      | Jamesia americana                               | 2070                | 3700                | Š           | INT                        |
| Lamiaceae          | Monardella beneolens                            | 2500                | 3600                | SS          | END                        |
| Lamiaceae          | Monardella linoides subsp.                      | 1000                | 3500                | SS          | INT ·                      |
| Lamiaceae          | Monardella odoratissima<br>subsp. glauca        | 1000                | 3500                | SS          | INT                        |
| Linaceae           | Linum lewisii                                   | 400                 | 3657                | P           | INT                        |
| Montiaceae         | Calyptridium monospermum                        | 300                 | 3970                | P           | INT                        |
| Montiaceae         | Calyptridium roseum                             | 1500                | 3800                | A           | CORD                       |
| Montiaceae         | Calyptridium umbellatum                         | 240                 | 4300                | P           | CORD                       |
| Montiaceae         | Claytonia nevadensis                            | 2200                | 3500                | P           | S-C                        |
| Montiaceae         | Lewisia disepala                                | 1300                | 3500                | P           | END                        |
| Montiaceae         | Lewisia glandulosa                              | 3000                | 4000                | P           | END-CAL                    |
| Montiaceae         | Lewisia nevadensis                              | 609                 | 3596                | P           | S-C                        |
| Montiaceae         | Lewisia pygmaea                                 | 1700                | 4020                | P           | CORD                       |
| Montiaceae         | Lewisia triphylla                               | 1300                | 3500                | P           | CORD                       |
| Montiaceae         | Montia chamissoi                                | 1100                | 3700                | P           | S-C                        |
| Onagraceae         | Epilobium anagallidifolium                      | 1500                | 4500                | P           | WIDE                       |
| Onagraceae         | Epilobium ciliatum subsp.                       | 0                   | 4000                | P           | CORD                       |
| Onagraceae         | Epilobium ciliatum subsp. glandulosum           | 0                   | 3500                | P           | WIDE                       |
| Onagraceae         | Epilobium clavatum                              | 1200                | 4200                | P           | CORD                       |
| Onagraceae         | Epilobium glaberrimum subsp. fastigiatum        | 1200                | 3800                | P           | CORD                       |
| Onagraceae         | Epilobium hallianum                             | 100                 | 3700                | P           | CORD                       |
| Onagraceae         | Épilobium hornemannii                           | 1200                | 3900                | P           | WIDE                       |
| Onagraceae         | subsp. hornemannii<br>Epilobium obcordatum      | 1700                | 4000                | P           | S-C                        |
| Onagraceae         | Epilobium oregonense                            | 1200                | 3500                | P           | CORD                       |
| Onagraceae         | Epilobium saximontanum                          | 1400                | 3500                | P           | CORD                       |
| Onagraceae         | Gayophytum decipiens                            | 1800                | 4200                | Ā           | INT                        |
| Onagraceae         | Gayophytum diffusum subsp.                      | 800                 | 3700                | A           | S-C                        |
|                    | diffusum  | 200                 | 2.00                | - *         |                            |

| Specific or Inflarespecific taxon   Specific or Inflarespecific or Inflarespec   | Appendix 1. Continued. |                                 |      |      |              |                |  |
|--|------------------------|---------------------------------|------|------|--------------|----------------|--|
| Onagraceae         Gayophytum racemosum         1000         4000         A         CORD           Onagraceae         Gayophytum racemosum         500         3500         A         INT           Orobanchaceae         Castilleja applegatei subsp.         300         3600         P         INT           Orobanchaceae         Castilleja applegatei subsp.         1500         3500         P         INT           Orobanchaceae         Castilleja mmidat subsp.         1500         3500         P         INT           Orobanchaceae         Castilleja mmidat subsp.         1500         3500         P         INT           Orobanchaceae         Castilleja mmidat subsp.         1500         3500         P         INT           Orobanchaceae         Castilleja minidat subsp.         1500         4000         P         S-C           Orobanchaceae         Peleciularis stonelludias         1500         3500         P         S-C           Orobanchaceae         Peleciularis stonelludias         1500         3500         P         S-C           Orobanchaceae         Peleciularis stonelludias         1500         3500         P         S-C           Orabanchaceae         Peleciularis stonelludias         1500   | Higher level taxor     |                                 |      |      |              |                |  |
| Onagraceae         Gayophytum ramossissimm         500         3500         A         INT           Onbanchaceae         Gayophytum ramossissimm         500         3500         P         INT           Orobanchaceae         Castilleja applegatet subsp. pallida         300         3600         P         INT           Orobanchaceae         Castilleja imilata subsp. pallida         1500         3500         P         INT           Orobanchaceae         Castilleja imilata subsp. pallida         1500         3500         P         INT           Orobanchaceae         Castilleja imilata subsp. pelidia milata subsp. pelidia p  | Onagraceae             |                                 | 800  | 3700 | A            | INT            |  |
| Orobanchaceae         castille/a applegatei subsp. pallillab         1900         3600         P         INT           Orobanchaceae         Castille/a applegatei subsp. pintorum         300         3600         P         INT           Orobanchaceae         Castille/a miniata subsp. miniata         1500         3500         P         INT           Orobanchaceae         Castille/a miniata subsp. miniata         1500         3500         P         END-CAL           Orobanchaceae         Crostille/a miniata subsp. miniata         1200         4000         P         S-C           Orobanchaceae         Pedeclularis strollens         1200         4000         P         S-C           Orobanchaceae         Pedeclularis strollens         100         3600         P         S-C           Orobanchaceae         Pedeclularis strollens         100         3600         P         S-C           Orobanchaceae         Pedeclularis strollens         100         3600         P         WIDE           Plantaginaceae         Pedeclularis strollens         1100         4000         A         INT           Plantaginaceae         Penstemon davidsonii         200         3750         P-MAT         INT           Plantaginaceae         Penstemo  | Onagraceae             |                                 | 1000 | 4000 | Α            | CORD           |  |
| Orobanchaceae         Castille applegate is ubsp. pibetorum         300         3600         P         INT           Orobanchaceae         Castille applegate is ubsp. pibetorum         1550         3700         P         S.C           Orobanchaceae         Castille aminiata subsp. miniata         1500         3500         P         INT           Orobanchaceae         Pedicularis attollens         1200         4000         P         S.C           Orobanchaceae         Pedicularis genotlandica         1000         3600         P         S.C           Orobanchaceae         Pedicularis sembarbata         1500         3500         P         S.C           Orobanchaceae         Pedicularis sembarbata         1500         3500         P         S.C           Parnassiaceae         Pedicularis sembarbata         1500         3500         P         S.C           Parrassiaceae         Parmassia palustris         0         3600         P         WIDE           Plantaginaceae         Polatriche palustris         0         4000         Q         WIDE           Plantaginaceae         Penstemon heterodoxus var.         2700         3900         P.MAT         INT           Plantaginaceae         Penstemon newherryi var.  | Onagraceae             | Gayophytum ramosissimum         | 500  | 3500 | Α            | INT            |  |
| Orobanchaceae         Castilleja applegatei subsp. pibitorium         300         P         INT           Orobanchaceae         Castilleja lemimonii         1550         3700         P         S.C           Orobanchaceae         Castilleja miniata subsp. miniata         1500         3500         P         INT           Orobanchaceae         Crostilleja miniata         2400         4200         P         END-CAL           Orobanchaceae         Pedicularis attollens         1200         4000         P         S-C           Orobanchaceae         Pedicularis stronibaria         1500         3500         P         S-C           Parnassicaeae         Pelatriaginaceae         Pelatriaginaceae         Pelatriaginaceae         Pelatriaginaceae         Periloridoris sembarbata         1500         3500         P         S-C           Plantaginaceae         Plantaginaceae         Penstemon davisonii         2000         3500         A         WIDE           Plantaginaceae         Plantaginaceae         Penstemon deverodoxis var.         2700         3900         P-MAT         INT           Plantaginaceae         Penstemon revisitoris         200         3500         SS         INT           Plantaginaceae         Penstemon roceris var.         <   |                        |                                 | 1900 | 3600 | P            | INT            |  |
| Orobanchaceae         Castilleja minataa subsp. minitaa         1500         3500         P         INT           Orobanchaceae         Corobanchaceae         Pedicularis attollens         1200         4200         P         END-CAL           Orobanchaceae         Pedicularis attollens         1200         4000         P         S-C           Orobanchaceae         Pedicularis genelandica         1000         3600         P         S-C           Orobanchaceae         Pedicularis genelandica         1000         3600         P         S-C           Parnassiaceae         Parnassia pansitris         0         3600         P         WIDE           Plantaginaceae         Calliris pansitris         0         4000         Q         WIDE           Plantaginaceae         Collinsia parvilora         800         3500         A         WIDE           Plantaginaceae         Pensiennon davidsonii         2000         3750         P.MAT         INT           Plantaginaceae         Pensiennon newberryi var.         1000         3700         P-MAT         INT           Plantaginaceae         Pensiennon procerus var.         2100         3600         P-MAT         INT           Plantaginaceae         Pensiennon roserillorus   | Orobanchaceae          |                                 | 300  | 3600 | P            | INT            |  |
| minitata         Author         Author         P         END-CAL           Orobanchaceae         Pedicularis atolleus         1200         4000         P         S-C           Orobanchaceae         Pedicularis groenlandica         1000         3600         P         S-C           Orobanchaceae         Pedicularis sembarbata         1500         3500         P         S-C           Parnassiaceae         Permissia palistris         0         3600         P         WIDE           Plantaginaceae         Ministria suksidofii         1100         4000         Q         WIDE           Plantaginaceae         Collusia parvillora         800         3500         A         MIDE           Plantaginaceae         Penstemon davidsonii         2000         3750         P-MAT         INT           Plantaginaceae         Penstemon davidsonii         2000         3700         P-MAT         INT           Plantaginaceae         Penstemon newberryi var.         1000         3700         P-MAT         INT           Plantaginaceae         Penstemon prostriflorus         500         3500         SS         INT           Plantaginaceae         Penstemon rostriflorus         500         3500         P         INT<   | Orobanchaceae          | Castilleja lemmonii             | 1550 | 3700 | P            | S-C            |  |
| Orobanchaceae         Pedicularis attollens         1200         4000         P         S-C           Orobanchaceae         Pedicularis geneilhandica         1000         3500         P         S-C           Parnassiaceae         Pedravasia palustris         0         3600         P         WIDE           Phrymaceae         Parnassia palustris         0         4000         A         INT           Plantaginaceae         Calliris parvillora         800         3500         A         WIDE           Plantaginaceae         Calliris parvillora         800         3500         A         WIDE           Plantaginaceae         Collisis parvillora         800         3500         A         MIT           Plantaginaceae         Penstemon davidsonii         2000         3750         P-MAT         INT           Plantaginaceae         Penstemon beterodoxus var.         2700         3900         P-MAT         INT           Plantaginaceae         Penstemon beterryi var.         1000         3700         P-MAT         INT           Plantaginaceae         Penstemon rostriflorus         500         3500         SS         INT           Plantaginaceae         Penstemon rostriflorus         500         3500   | Orobanchaceae          |                                 | 1500 | 3500 | P            | INT            |  |
| Orobanchaceae         Pedicularis genelandica         1000         3600         P         S-C           Orobanchaceae         Pedicularis semibarbata         1500         3500         P         S-C           Parnassiaceae         Parnassia palustris         0         3600         P         WIDE           Phrymaceae         Minuhas suksdorfii         1100         4000         Q         WIDE           Plantaginaceae         Collinsia parvillora         800         3500         A         WIDE           Plantaginaceae         Collinsia torrevi var. wrightii         800         3500         A         WIDE           Plantaginaceae         Penstemon devodoxis var. heterodoxis         2700         3900         P-MAT         INT           Plantaginaceae         Penstemon procerus var. heterodoxis         1000         3600         P-MAT         INT           Plantaginaceae         Penstemon procerus var. formosus         2100         3600         P-MAT         INT           Plantaginaceae         Penstemon restriflorus         500         3500         SS         INT           Plantaginaceae         Penstemon restriflorus         500         3500         SS         INT           Plantaginaceae         Penstemon rescriflorus<  | Orobanchaceae          | Castilleja nana                 | 2400 | 4200 | P            | <b>END-CAL</b> |  |
| Orobanchaceae         Pedicularis semibarbata         1500         3500         P         S-C           Parnassiacae         Minuhas suksdorfii         1100         4000         A         INT           Plantaginaceae         Callitriche palustris         0         4000         A         INT           Plantaginaceae         Collinist parviflora         800         3500         A         WIDE           Plantaginaceae         Collinist parviflora         800         4000         A         INT           Plantaginaceae         Penstemon davidsonii         2000         3750         P-MAT         INT           Plantaginaceae         Penstemon devidsonii         2000         3700         P-MAT         INT           Plantaginaceae         Penstemon newberryi var.         1000         3700         P-MAT         INT           Plantaginaceae         Penstemon procerus var.         2100         3600         P-MAT         INT           Plantaginaceae         Penstemon revelergii var.         1000         3500         SS         INT           Plantaginaceae         Penstemon revelergii var.         1000         3600         P         INT           Plantaginaceae         Penstemon revelergii var.         1000   | Orobanchaceae          | Pedicularis attollens           | 1200 | 4000 | P            | S-C            |  |
| Parnassiaceae  | Orobanchaceae          | Pedicularis groenlandica        | 1000 | 3600 | P            | S-C            |  |
| Phrymaceae   | Orobanchaceae          | Pedicularis semibarbata         | 1500 | 3500 | P            | S-C            |  |
| Plantaginaceae   Callitriche palustris   0   4000   Q   WIDE   | Parnassiaceae          | Parnassia palustris             | 0    | 3600 | P            | WIDE           |  |
| Plantaginaceae   Callitriche palustris   0   4000   Q   WIDE   | Phrymaceae             | Mimulus suksdorfii              | 1100 | 4000 | $\mathbf{A}$ | INT            |  |
| Plantaginaceae   Collinsia parvilfora   800   3500   A   NIT   | Plantaginaceae         |                                 | 0    | 4000 | Q            | WIDE           |  |
| Plantaginaceae   Penstemon davidsonii   2000   3750   P.MAT   INT  | Plantaginaceae         | Collinsia parviflora            | 800  | 3500 |              | WIDE           |  |
| Plantaginaceae   |                        | Collinsia torreyi var. wrightii | 800  | 4000 | A            | INT            |  |
| Plantaginaceae   |                        |                                 | 2000 | 3750 | P-MAT        | INT            |  |
| Pantaginaceae  |                        |                                 | 2700 | 3900 |              | S-C            |  |
| Plantaginaceae   | Plantaginaceae         | Penstemon newberryi var.        | 1000 | 3700 | P-MAT        | INT            |  |
| Plantaginaceae   | Plantaginaceae         | Penstemon procerus var.         | 2100 | 3600 | P-MAT        | INT            |  |
| Plantaginaceae   | Plantaginaceae         | Penstemon roezlii               | 300  | 3500 | SS           | INT            |  |
| Plantaginaceae Penstemon rydbergii var. oreocharis  Plantaginaceae Penstemon speciosus 850 3800 P INT  Plantaginaceae Veronica wormskjoldii 1500 3500 P WIDE  Polemoniaceae Collomia linearis 600 3500 A WIDE  Polemoniaceae Gymnosteris parvula 2400 3700 A CORD  Polemoniaceae Ipomopsis congesta subsp. 1500 3700 P S-C  montana  Polemoniaceae Leptosiphon oblanceolatus 2800 3700 A END  Polemoniaceae Linanthus pungens 1700 4000 P CORD  Polemoniaceae Phlox diffusa 1100 3600 P-MAT CORD  Polemoniaceae Phlox diffusa 1100 3600 P-MAT CORD  Polemoniaceae Phlox dispersa 3600 4200 P-MAT END  Polemoniaceae Phlox pulvinata 3300 4300 P-MAT CORD  Polemoniaceae Polemonium eximium 3000 4200 P END  Polemoniaceae Polemonium pulcherrimum 2400 3700 P S-C  var. pulcherrimum  Polygonaceae Eriogonum gracilipes 2900 3900 P-MAT END-CAL  Polygonaceae Eriogonum nudum var. 2800 3800 P-MAT END  Polygonaceae Eriogonum nudum var. 2800 3800 P-MAT END  Polygonaceae Eriogonum ovalifolium var. 2800 3800 P-MAT END  Polygonaceae Eriogonum ovalifolium var. 2800 3500 P-MAT END  Polygonaceae Eriogonum nolypodum 2800 3500 P-MAT END  Polygonaceae Eriogonum polypodum 2800 3500 P-MAT END  Polygonaceae Eriogonum spergulimum var. 2300 4000 P-MAT INT  rosense  Polygonaceae Eriogonum spergulimum var. 3000 3600 P-MAT END  Polygonaceae Eriogonum umbellatum var. 3000 3600 P-MAT END  Polygonaceae Eriogonum umbellatum var. 3000 3600 P-MAT END-CAL  Friogonum wrightii var. 3000 3600 P-MAT END-CAL  |                        | Penstemon rostriflorus          | 500  | 3500 | SS           | INT            |  |
| Plantaginaceae   |                        | Penstemon rydbergii var.        | 1000 | 3600 | P            | INT            |  |
| Plantaginaceae   | Plantaginaceae         |                                 | 850  | 3800 | P            | INT            |  |
| Polemoniaceae Collomia linearis 600 3650 A WIDE Polemoniaceae Gymnosteris parvula 2400 3700 A CORD Polemoniaceae Ipomopsis congesta subsp. 1500 3700 P S-C montana Polemoniaceae Leptosiphon oblanceolatus 2800 3700 A END Polemoniaceae Linanthus pungens 1700 4000 P CORD Polemoniaceae Phlox condensata 2000 4000 P-MAT CORD Polemoniaceae Phlox diffusa 1100 3600 P-MAT CORD Polemoniaceae Phlox dispersa 3600 4200 P-MAT END Polemoniaceae Phlox pulvinata 3300 4300 P-MAT CORD Polemoniaceae Polemonia |                        |                                 |      |      |              |                |  |
| Polemoniaceae   Gymnosteris parvula   2400   3700   A   CORD   |                        |                                 |      |      |              |                |  |
| Polemoniaceae Ipomopsis congesta subsp. montana  Polemoniaceae Leptosiphon oblanceolatus 2800 3700 A END Polemoniaceae Limanthus pungens 1700 4000 P CORD Polemoniaceae Phlox condensata 2000 4000 P-MAT CORD Polemoniaceae Phlox diffusa 1100 3600 P-MAT CORD Polemoniaceae Phlox dispersa 3600 4200 P-MAT END Polemoniaceae Phlox pulvinata 3300 4300 P-MAT CORD Polemoniaceae Polemonium eximium 3000 4200 P END Polemoniaceae Polemonium eximium 3000 4200 P END Polemoniaceae Polemonium pulcherrimum 2400 3700 P S-C var. pulcherrimum Polygonaceae Eriogonum gracilipes 2900 3900 P-MAT END-CAL Polygonaceae Eriogonum lobbii 1600 3800 P-MAT S-C Polygonaceae Eriogonum nudum var. 2800 3800 P END  Polygonaceae Eriogonum ovalifolium var. 3000 3600 P-MAT END Polygonaceae Eriogonum ovalifolium var. 1700 4200 P-MAT END Polygonaceae Eriogonum ovalifolium var. 2300 3500 P-MAT END Polygonaceae Eriogonum polypodum 2800 3500 P-MAT END Polygonaceae Eriogonum rosense var. 2300 4000 P-MAT INT  Polygonaceae Eriogonum polypodum 2800 3500 P-MAT END Polygonaceae Eriogonum spergulinum var. 1300 3500 P-MAT END Polygonaceae Eriogonum spergulinum var. 3000 3600 P-MAT END Polygonaceae Eriogonum wrightii var. 3000 3600 P-MAT END-CAL  Polygonaceae Eriogonum wrightii var. 3500 3600 P-MAT END-CAL  |                        |                                 |      |      |              |                |  |
| Polemoniaceae Leptosiphon oblanceolatus 2800 3700 A END Polemoniaceae Linanthus pungens 1700 4000 P CORD Polemoniaceae Phlox condensata 2000 4000 P-MAT CORD Polemoniaceae Phlox diffusa 1100 3600 P-MAT CORD Polemoniaceae Phlox diffusa 3600 4200 P-MAT CORD Polemoniaceae Phlox dispersa 3600 4200 P-MAT CORD Polemoniaceae Phlox pulvinata 3300 4300 P-MAT CORD Polemoniaceae Polemonium eximium 3000 4200 P END Polemoniaceae Polemonium eximium 2400 3700 P S-C Var. pulcherrimum Polygonaceae Priogonum gracilipes 2900 3900 P-MAT END-CAL Polygonaceae Eriogonum incanum 2100 4000 P-MAT INT Polygonaceae Eriogonum incanum 2100 3800 P-MAT S-C Polygonaceae Eriogonum nudum var. 2800 3800 P END Scapigerum Polygonaceae Eriogonum ovalifolium var. 3000 3600 P-MAT END caelestinum Polygonaceae Eriogonum ovalifolium var. 2800 3500 P-MAT END Polygonaceae Eriogonum ovalifolium var. 3000 3500 P-MAT END Polygonaceae Eriogonum polypodum 2800 3500 P-MAT END Polygonaceae Eriogonum spergulinum var. 3000 3500 P END Pratense Polygonaceae Eriogonum wrightii var. 3000 3600 P-MAT END Polygonaceae Eriogonum wrightii var. 3000 3600 P-MAT END Polygonaceae Eriogonum wrightii var. 3000 3600 P-MAT END  |                        | Ipomopsis congesta subsp.       |      |      |              |                |  |
| Polemoniaceae Linanthus pungens 1700 4000 P CORD Polemoniaceae Phlox condensata 2000 4000 P-MAT CORD Polemoniaceae Phlox diffusa 1100 3600 P-MAT CORD Polemoniaceae Phlox dispersa 3600 4200 P-MAT END Polemoniaceae Phlox pulvinata 3300 4300 P-MAT CORD Polemoniaceae Phlox pulvinata 3300 4300 P-MAT CORD Polemoniaceae Polemonium eximium 3000 4200 P END Polemoniaceae Polemonium pulcherrimum 2400 3700 P S-C var. pulcherrimum Polygonaceae Eriogonum gracilipes 2900 3900 P-MAT END-CAL Polygonaceae Eriogonum incanum 2100 4000 P-MAT INT Polygonaceae Eriogonum lobbii 1600 3800 P-MAT INT Polygonaceae Eriogonum nudum var. 2800 3800 P-MAT S-C Polygonaceae Eriogonum ovalifolium var. 3000 3600 P-MAT END caelestimum Polygonaceae Eriogonum ovalifolium var. 1700 4200 P-MAT INT nivale Polygonaceae Eriogonum polypodum 2800 3500 P-MAT END Polygonaceae Eriogonum rosense var. 2300 4000 P-MAT INT INT nivale Polygonaceae Eriogonum spergulinum var. 1300 3500 P-MAT END Polygonaceae Eriogonum spergulinum var. 1300 3500 P-MAT END Polygonaceae Eriogonum spergulinum var. 1300 3500 P END Pratense Polygonaceae Eriogonum unbellatum var. 3000 3600 P-MAT END Polygonaceae Eriogonum wrightii var. 3000 3600 P-MAT END Polygonaceae Eriogonum wrightii var. 3000 3600 P-MAT END END Polygonaceae Eriogonum wrightii var. 3000 3600 P-MAT END END-CAL covillei  | Polemoniaceae          |                                 | 2800 | 3700 | Α            | END            |  |
| Polemoniaceae Phlox condensata 2000 4000 P-MAT CORD Polemoniaceae Phlox diffusa 1100 3600 P-MAT CORD Polemoniaceae Phlox dispersa 3600 4200 P-MAT END Polemoniaceae Phlox pulvinata 3300 4300 P-MAT CORD Polemoniaceae Phlox pulvinata 3300 4200 P-MAT CORD Polemoniaceae Polemonium eximium 3000 4200 P END Polemoniaceae Polemonium pulcherrimum 2400 3700 P S-C Var. pulcherrimum 2400 3700 P S-C Var. pulcherrimum 2400 3700 P-MAT END-CAL Polygonaceae Eriogonum gracilipes 2900 3900 P-MAT INT Polygonaceae Eriogonum lobbii 1600 3800 P-MAT S-C Polygonaceae Eriogonum nudum var. 2800 3800 P END Scapigerum Polygonaceae Eriogonum ovalifolium var. 2800 3800 P-MAT END Caclestinum Polygonaceae Eriogonum ovalifolium var. 2800 3500 P-MAT INT Nivale Polygonaceae Eriogonum polypodum 2800 3500 P-MAT INT Nivale Polygonaceae Eriogonum spergulinum var. 2300 4000 P-MAT INT Novente Polygonaceae Eriogonum spergulinum var. 2300 3500 P-MAT END Polygonaceae Eriogonum spergulinum var. 3000 3500 P-MAT END Polygonaceae Eriogonum spergulinum var. 3000 3500 P-MAT END Polygonaceae Eriogonum unbellatum var. 3000 3500 P-MAT END Polygonaceae Eriogonum wrightii var. 3000 3600 P-MAT END END Polygonaceae Eriogonum wrightii var. 3000 3600 P-MAT END END Polygonaceae Eriogonum wrightii var. 3500 3600 P-MAT END END Polygonaceae Eriogonum wrightii var. 3500 3600 P-MAT END  |                        |                                 |      |      |              |                |  |
| Polemoniaceae Phlox diffusa 1100 3600 P-MAT CORD Polemoniaceae Phlox dispersa 3600 4200 P-MAT END Polemoniaceae Phlox pulvinata 3300 4300 P-MAT CORD Polemoniaceae Polemonium eximium 3000 4200 P END Polemoniaceae Polemonium pulcherrimum 2400 3700 P S-C var. pulcherrimum 2400 3700 P-MAT END-CAL Polygonaceae Eriogonum gracilipes 2900 3900 P-MAT INT Polygonaceae Eriogonum incanum 2100 4000 P-MAT INT Polygonaceae Eriogonum lobbii 1600 3800 P-MAT S-C Polygonaceae Eriogonum ovalifolium var. 2800 3800 P-MAT END scapigerum Polygonaceae Eriogonum ovalifolium var. 3000 3600 P-MAT END Polygonaceae Eriogonum ovalifolium var. 1700 4200 P-MAT INT nivale Polygonaceae Eriogonum rosense var. 2300 4000 P-MAT INT rosense Polygonaceae Eriogonum spergulinum var. 1300 3500 P-MAT END Polygonaceae Eriogonum spergulinum var. 3000 3600 P-MAT END Polygonaceae Eriogonum spergulinum var. 3000 3500 P-MAT END Polygonaceae Eriogonum spergulinum var. 3000 3500 P-MAT END Polygonaceae Eriogonum spergulinum var. 3000 3500 P-MAT END Polygonaceae Eriogonum mbellatum var. 3000 3600 P-MAT END Polygonaceae Eriogonum wiphtii var. 3000 3600 P-MAT END-CAL covillei  |                        |                                 |      |      |              |                |  |
| Polemoniaceae Phlox dispersa 3600 4200 P-MAT END Polemoniaceae Phlox pulvinata 3300 4300 P-MAT CORD Polemoniaceae Phlox pulvinata 3300 4200 P END Polemoniaceae Polemonium eximium 3000 4200 P END Polemoniaceae Polemonium pulcherrimum 2400 3700 P S-C var. pulcherrimum Polygonaceae Eriogonum gracilipes 2900 3900 P-MAT END-CAL Polygonaceae Eriogonum incanum 2100 4000 P-MAT INT Polygonaceae Eriogonum nudum var. 2800 3800 P END Scapigerum Polygonaceae Eriogonum nudum var. 3000 3600 P-MAT END Polygonaceae Eriogonum ovalifolium var. 1700 4200 P-MAT INT END caelestinum Polygonaceae Eriogonum ovalifolium var. 2800 3500 P-MAT END Polygonaceae Eriogonum rosense var. 2300 4000 P-MAT INT rosense Polygonaceae Eriogonum spergulinum var. 1300 3500 P-MAT INT rosense Polygonaceae Eriogonum spergulinum var. 3000 3600 P-MAT END Polygonaceae Eriogonum spergulinum var. 3000 3500 P-MAT END Polygonaceae Eriogonum umbellatum var. 3000 3600 P-MAT END Polygonaceae Eriogonum umbellatum var. 3000 3600 P-MAT END Polygonaceae Eriogonum umbellatum var. 3000 3600 P-MAT END-CAL covillei   |                        |                                 |      |      |              |                |  |
| Polemoniaceae Phlox pulvinata 3300 4300 P-MAT CORD Polemoniaceae Polemonium eximium 3000 4200 P END Polemoniaceae Polemonium eximium 2400 3700 P S-C var. pulcherrimum 2400 3700 P S-C var. pulcherrimum 2400 3700 P S-C var. pulcherrimum 2400 3700 P-MAT END-CAL Polygonaceae Eriogonum gracilipes 2900 3900 P-MAT INT Polygonaceae Eriogonum incanum 2100 4000 P-MAT INT Polygonaceae Eriogonum lobbii 1600 3800 P-MAT S-C Polygonaceae Eriogonum nudum var. 2800 3800 P END scapigerum 2800 3800 P END Scapigerum 2800 Sapigerum 2800 P-MAT END 2800 P-MAT INT END 2800 Sapigerum 2800 P-MAT INT 28000 P-MAT INT 28000 P-MAT END 2800 P-M |                        |                                 |      |      |              |                |  |
| Polemoniaceae Polemonium eximium 3000 4200 P END 701 Polemoniaceae Polemonium pulcherrimum 2400 3700 P S-C 1701 Polygonaceae Eriogonum gracilipes 2900 3900 P-MAT END-CAL 1701 Polygonaceae Eriogonum incanum 2100 4000 P-MAT INT 1701 Polygonaceae Eriogonum nudum var. 2800 3800 P-MAT S-C 1701 Polygonaceae Eriogonum ovalifolium var. 2800 3800 P-MAT END 1801 Polygonaceae Eriogonum ovalifolium var. 3000 3600 P-MAT END 1801 Polygonaceae Eriogonum ovalifolium var. 1700 4200 P-MAT INT 1801 Polygonaceae Eriogonum polypodum 2800 3500 P-MAT END 1801 Polygonaceae Eriogonum rosense var. 2300 4000 P-MAT INT 1801 Polygonaceae Eriogonum spergulinum var. 1300 3500 P-MAT INT 1801 Polygonaceae Eriogonum spergulinum var. 1300 3500 P-MAT END 1801 Polygonaceae Eriogonum spergulinum var. 1300 3500 P-MAT END 1801 Polygonaceae Eriogonum umbellatum var. 3000 3600 P-MAT END 1801 Polygonaceae Eriogonum umbellatum var. 3000 3600 P-MAT END-CAL 1801 Polygonaceae Eriogonum wrightii var. 3500 3600 P-MAT END-CAL 1801 Polygonaceae Eriogonum wrightii var. 3500 3600 P-MAT END  |                        |                                 |      |      |              |                |  |
| Polemoniaceae Polemonium pulcherrimum var. pulcherrimum polygonaceae P |                        |                                 |      |      |              |                |  |
| Polygonaceae Eriogonum gracilipes 2900 3900 P-MAT END-CAL Polygonaceae Eriogonum incanum 2100 4000 P-MAT INT Polygonaceae Eriogonum lobbii 1600 3800 P-MAT S-C Polygonaceae Eriogonum nudum var. 2800 3800 P END  Scapigerum Polygonaceae Eriogonum ovalifolium var. 3000 3600 P-MAT END  Caelestinum Polygonaceae Eriogonum ovalifolium var. 1700 4200 P-MAT INT  nivale Polygonaceae Eriogonum polypodum 2800 3500 P-MAT END Polygonaceae Eriogonum rosense var. 2300 4000 P-MAT INT  rosense Polygonaceae Eriogonum spergulinum var. 1300 3500 P-MAT INT  Polygonaceae Eriogonum spergulinum var. 3000 3600 P-MAT END  Polygonaceae Eriogonum umbellatum var. 3000 3600 P-MAT END-CAL  covillei Polygonaceae Eriogonum wrightii var. 3500 3600 P-MAT END-CAL  |                        | Polemonium pulcherrimum         |      |      |              |                |  |
| Polygonaceae Eriogonum incanum 2100 4000 P-MAT INT Polygonaceae Eriogonum lobbii 1600 3800 P-MAT S-C Polygonaceae Eriogonum nudum var. 2800 3800 P END scapigerum Polygonaceae Eriogonum ovalifolium var. 3000 3600 P-MAT END caelestinum Polygonaceae Eriogonum ovalifolium var. 1700 4200 P-MAT INT nivale Polygonaceae Eriogonum polypodum 2800 3500 P-MAT END Polygonaceae Eriogonum rosense var. 2300 4000 P-MAT INT rosense Polygonaceae Eriogonum spergulinum var. 1300 3500 P-MAT INT pratense Polygonaceae Eriogonum umbellatum var. 3000 3600 P-MAT END pratense Polygonaceae Eriogonum wrightii var. 3500 3600 P-MAT END-CAL  | Polygonaceae           |                                 | 2900 | 3900 | P-MAT        | END-CAI        |  |
| Polygonaceae Eriogonum lobbii 1600 3800 P-MAT S-C Polygonaceae Eriogonum nudum var. 2800 3800 P END scapigerum  Polygonaceae Eriogonum ovalifolium var. 3000 3600 P-MAT END caelestinum  Polygonaceae Eriogonum ovalifolium var. 1700 4200 P-MAT INT nivale Polygonaceae Eriogonum polypodum 2800 3500 P-MAT END Polygonaceae Eriogonum rosense var. 2300 4000 P-MAT INT rosense  Polygonaceae Eriogonum spergulinum var. 1300 3500 P END pratense Polygonaceae Eriogonum umbellatum var. 3000 3600 P-MAT END-CAL covillei  Polygonaceae Eriogonum wrightii var. 3500 3600 P-MAT END   |                        |                                 |      |      |              |                |  |
| Polygonaceae Eriogonum nudum var. 2800 3800 P END scapigerum  Polygonaceae Eriogonum ovalifolium var. 3000 3600 P-MAT END caelestinum  Polygonaceae Eriogonum ovalifolium var. 1700 4200 P-MAT INT nivale  Polygonaceae Eriogonum polypodum 2800 3500 P-MAT END Polygonaceae Eriogonum rosense var. 2300 4000 P-MAT INT rosense  Polygonaceae Eriogonum spergulinum var. 1300 3500 P END pratense  Polygonaceae Eriogonum umbellatum var. 3000 3600 P-MAT END-CAL covillei  Polygonaceae Eriogonum wrightii var. 3500 3600 P-MAT END   |                        |                                 |      |      |              |                |  |
| Polygonaceae Eriogonum ovalifolium var. 3000 3600 P-MAT END caelestinum  Polygonaceae Eriogonum ovalifolium var. 1700 4200 P-MAT INT nivale  Polygonaceae Eriogonum polypodum 2800 3500 P-MAT END Polygonaceae Eriogonum rosense var. 2300 4000 P-MAT INT rosense  Polygonaceae Eriogonum spergulinum var. 1300 3500 P END pratense  Polygonaceae Eriogonum umbellatum var. 3000 3600 P-MAT END-CAL covillei  Polygonaceae Eriogonum wrightii var. 3500 3600 P-MAT END   |                        | Eriogonum nudum var.            |      |      |              |                |  |
| Polygonaceae Eriogonum ovalifolium var. 1700 4200 P-MAT INT nivale  Polygonaceae Eriogonum polypodum 2800 3500 P-MAT END Polygonaceae Eriogonum rosense var. 2300 4000 P-MAT INT rosense  Polygonaceae Eriogonum spergulinum var. 1300 3500 P END pratense  Polygonaceae Eriogonum umbellatum var. 3000 3600 P-MAT END-CAL covillei  Polygonaceae Eriogonum wrightii var. 3500 3600 P-MAT END-CAL  | Polygonaceae           | Eriogonum ovalifolium var.      | 3000 | 3600 | P-MAT        | END            |  |
| Polygonaceae Eriogonum polypodum 2800 3500 P-MAT END Polygonaceae Eriogonum rosense var. 2300 4000 P-MAT INT  rosense  Polygonaceae Eriogonum spergulinum var. 1300 3500 P END  pratense  Polygonaceae Eriogonum umbellatum var. 3000 3600 P-MAT END-CAL  covillei  Polygonaceae Eriogonum wrightii var. 3500 3600 P-MAT END   | Polygonaceae           | Eriogonum ovalifolium var.      | 1700 | 4200 | P-MAT        | INT            |  |
| Polygonaceae Eriogonum rosense var. 2300 4000 P-MAT INT rosense  Polygonaceae Eriogonum spergulinum var. 1300 3500 P END pratense  Polygonaceae Eriogonum umbellatum var. 3000 3600 P-MAT END-CAL covillei  Polygonaceae Eriogonum wrightii var. 3500 3600 P-MAT END   | Polygonaceae           |                                 | 2800 | 3500 | P-MAT        | END            |  |
| Polygonaceae Eriogonum spergulinum var. 1300 3500 P END  pratense  Polygonaceae Eriogonum umbellatum var. 3000 3600 P-MAT END-CAL  covillei  Polygonaceae Eriogonum wrightii var. 3500 3600 P-MAT END  |                        | Eriogonum rosense var.          |      |      |              |                |  |
| Polygonaceae Eriogonum umbellatum var. 3000 3600 P-MAT END-CAL covillei Polygonaceae Eriogonum wrightii var. 3500 3600 P-MAT END   | Polygonaceae           | Eriogonum spergulinum var.      | 1300 | 3500 | P            | END            |  |
|  | Polygonaceae           | Eriogonum umbellatum var.       | 3000 | 3600 | P-MAT        | END-CAL        |  |
|  | Polygonaceae           | Eriogonum wrightii var.         | 3500 | 3600 | P-MAT        | END            |  |

| Higher level taxon   |                    |                                 | NDIX I. CONTI |                     |       |                            |
|--|--------------------|---------------------------------|---------------|---------------------|-------|----------------------------|
| Polygonaceae         Rumex californicas         0         5500         P         COR           Polygonaceae         Rumex paucifolius         1500         4000         P         COR           Polygonaceae         Rumex sulicifolius         0         3500         P         CNR           Polygonaceae         Rumex sulicifolius         1000         3500         P         CNR           Primulaceae         Dodecatheon subdiphum         2100         4000         P         ENT           Primulaceae         Polaceatheon subdiphum         2100         4000         P         ENT           Primulaceae         Pellaca brewer         1500         3700         P         ENT           Primulaceae         Pellaca brewer         1500         3700         P         ENT           Ranuculaceae         Acontum columbihumm         300         3500         P         ENT           Ranuculaceae         Ramuculaceae         Ramuculaceae         Aguity publica pubescens         2500         3650         P         ENT           Ranuculaceae         Ramuculaceae         Ramuculaceae         Ramuculaceae         Ramuculaceae         Ramuculaceae         Ramuculaceae         Ramuculaceae         Ramuculaceae         Ramuculac   | Higher level taxon | Specific or infraspecific taxon |               | Upper elevation (m) |       | Biogeographic relationship |
| Polygonaceae   | Polygonaceae       | Oxyria digyna                   | 1800          | 4000                | P     | WIDE                       |
| Polygonaceae   | Polygonaceae       | Rumex californicus              | 0             | 3500                | P     | CORD                       |
| Polygonaceae   | Polygonaceae       | Rumex paucifolius               | 1500          | 4000                | P     | S-C                        |
| Polygonaceae   Rumex utahensis   1000   3500   P   COR   Primulaceae   Androsace septentrionalis   2700   3600   P   NT   Primulaceae   Dodecatheon redolens   2400   3600   P   NT   Primulaceae   Dodecatheon subalpinum   2100   4000   P   ENE   Primulaceae   Dodecatheon subalpinum   2100   4000   P   ENE   Primulaceae   Primula sulfrinescens   2000   4200   P   ENE   Primulaceae   Primula sulfrinescens   2000   4200   P   ENE   Primulaceae   Primula sulfrinescens   2000   3700   P   ENE   Ranunculaceae   Primula sulfrinescens   2000   3700   P   ENE   Subsp. columbianum   300   3500   P   ENE   Ranunculaceae   Aquilegia pubescens   2200   3600   P   ENE   Ranunculaceae   Ranunculas alismifolius var.   1400   3600   P   ENE   Administration   2200   3600   P   ENE   2300   2300   P   EN | Polygonaceae       | Rumex salicifolius              | 0             | 3500                | P     | INT                        |
| Primulaceae         Androsace septentrionalis         2700         3600         P.A.         WILP           Primulaceae         Dodecatheon redolors         2400         3600         P.         INT           Primulaceae         Podecatheon subalpinum         2100         4000         P.         ENE           Primulaceae         Primula sulfrutesvers         2000         4200         P.         ENE           Picaceae         Pellacu breweri         1500         3700         P.         ENE           Ranunculaceae         Aconitum columbianum         300         3500         P.         ENE           Ranunculaceae         Aguilegia pubescens         2600         3650         P.         ENE           Ranunculaceae         Ranunculus adualismifolius var.         200         3600         P.         S.C           Ranunculaceae         Ranunculus eschscholtzii var.         200         3600         P.         ENE           Ranunculaceae         Ranunculus eschscholtzii var.         2700         4300         P.         ENE           Ranunculaceae         Ranunculaceae         Ranunculaceae         Ranunculaceae         Ranunculaceae         Ranunculaceae         Ranunculaceae         Ranunculaceae         Publicaculaceae  |                    |                                 | 1000          | 3500                | P     | CORD                       |
| Primulaceae         Dodecatheon redolens         2400         3600         P         INT           Primulaceae         Dodecatheon subalpinum         2100         4000         P         ENT           Primulaceae         Primula suffratescens         2000         4200         P         ENT           Petridaceae         Pellacu breweri         1500         3700         P         INT           Ranunculaceae         Pellacu breweri         1500         3700         P         INT           Ranunculaceae         Aquileiga pubescens         2600         3650         P         ENT           Ranunculaceae         Ranunculas elismiolius var.         1400         3600         P         ENT           Ranunculaceae         Ramunculus eschscholtzii var.         2200         3600         P         ENT           Ranunculaceae         Ramunculus glaberrimus         1200         3600         P         ENT           Ranunculaceae         Ramunculaceae         Ramunculus glaberrimus         1200         3600         P         COR           Ranunculaceae         Thalictrum apparsiforum         1400         3500         P         COR           Ranunculaceae         Daymocaulis beudorupestris         3200  |                    |                                 |               | 3600                | P-A   | WIDE                       |
| Primulaceae         Dodecatheon subalpinum         2100         4000         P         ENT           Petridaceae         Primulaceae         Pollacea brewere         1500         3700         P         INT           Ranunculaceae         Aconitum columbianum         300         3500         P         COR           Ranunculaceae         Aquilegia pubescens         2600         3650         P         ENT           Ranunculaceae         Aquilegia pubescens         2600         3650         P         ENT           Ranunculaceae         Ramunculas alismifolius var.         1400         3600         P         S-C           Ranunculaceae         Ramunculas exekscholtzii var.         2200         3600         P         S-C           Ranunculaceae         Ramunculas exeksischoltzii var.         2700         4300         P         ENE           Ranunculaceae         Ramunculaceae         Ramunculaceae         Talicitrum alpinum         2900         3600         P         COR           Rosaceae         Drymocaulis suchea var.         1800         3700         P         WIE           Rosaceae         Drymocaulis pseudorupestris         2300         3900         P         COR           Rosaceae         <   |                    |                                 |               |                     |       |                            |
| Primulaceae         Primula suffruescens         2000         4200         P         ENC           Peteridaceae         Peluea breweri         1500         3700         P         INT           Ranunculaceae         Aconitum columbianum         300         3500         P         ENC           Ranunculaceae         Aquilegia pubescens         2600         3650         P         ENI           Ranunculaceae         Rumuculaceae Rumuculus adismfolius var.         1400         3600         P         S-C           Ranunculaceae         Ramunculus schscholtzii var.         2200         3600         P         S-C           Ranunculaceae         Ramunculas schscholtzii var.         2700         4300         P         ENE           Ranunculaceae         Ranunculas schscholtzii var.         2700         4300         P         ENE           Ranunculaceae         Ranunculas geberrimus         1200         3600         P         COR           Ranunculaceae         Thalictrum alpinum         2900         3700         P         WIE           Ranunculaceae         Dryanocuulis peudorupestris         3200         3900         P         COR           Rosaceae         Drypnocuulis peudorupestris         2300   |                    |                                 |               |                     |       |                            |
| Petridaceae  |                    |                                 |               |                     |       | END-CAL                    |
| Ranunculaceae   Aconitum columbianum   Subsp. columbianum   Subsp. columbianum   Subsp. columbianum   Ranunculaceae   Aquilegia pubescens   2600   3650   P  |                    |                                 |               |                     |       |                            |
| Ranunculaceae         Aquilegia pubescens         2600         3650         P         ENT           Ranunculaceae         Delphinion polycladon         2200         3600         P         SC           Ranunculaceae         Ramunculus alismifolius var.         1400         3600         P         S-C           Ranunculaceae         Ramunculus eschscholtzii var.         2200         3600         P         S-C           Ranunculaceae         Ramunculus eschscholtzii var.         2700         4300         P         ENC           Ranunculaceae         Ramunculus eschscholtzii var.         2700         3600         P         COR           Ranunculaceae         Ramunculaseae         Ramunculaseae         Phalictrum alpinum         2900         3700         P         WIE           Rosaceae         Drymocaulis pascudorupestris         2000         3600         S         WIE           Rosaceae         Drymocaulis pseudorupestris         3200         3900         P         COR           Rosaceae         Drymocaulis pseudorupestris         2300         3500         P         COR           Rosaceae         Drymocaulis pseudorupestris         2300         3500         P         COR           Rosaceae         Pr  |                    | Aconitum columbianum            |               |                     |       | CORD                       |
| Ranunculaceae   Delphinium polycladom   2200   3600   P   S-C  | Danunaulaaaaa      |                                 | 2600          | 3650                | D     | END                        |
| Ranunculaceae   Ranunculas alismifolius var.   alismifolius var.   alismifolius var.   alismifolius var.   alismifolius var.   2200   3600   P   S-C   eschscholtzii   Ranunculaceae   Ranunculus eschscholtzii   var.   2700   4300   P   ENE   ENE   2700   23600   P   COR   Ranunculaceae   Ranunculus eschscholtzii   var.   2700   3600   P   COR   Ranunculaceae   Ranunculus glaberrimus   1200   3600   P   COR   Ranunculaceae   Thalictrum alpinum   2900   3700   P   COR   Ranunculaceae   Thalictrum sparsiflorum   1400   3500   P   COR   Rosaceae   Dasiphora fruticosa   2000   3600   S   WIE   Rosaceae   Drymocaulis pseudorupestris   3200   3900   P   COR   Var. cruminam   2700   270 |                    |                                 |               |                     |       | END-CAL                    |
| Ranunculaceae   Ranunculus eschscholtzii var.   2200   3600   P   S-C  |                    |                                 |               |                     |       |                            |
| Ranunculaceae   Thalictrum alpinum   2900   3700   P   WIE   Ranunculaceae   Thalictrum sparsiflorum   1400   3500   P   COR   Rosaceae   Dasiphora fruticosa   2000   3600   S   WIE   Rosaceae   Drymocaulis lactea var.   1800   3700   P   INT   Iactea   Rosaceae   Drymocaulis pseudorupestris   3200   3900   P   COR   Var. crumiana   Rosaceae   Drymocaulis pseudorupestris   2300   3500   P   COR   Var. saxicola   Rosaceae   Drymocaulis pseudorupestris   2300   3500   P   COR   Var. saxicola   Rosaceae   Holodiscus discolor var.   1159   4000   S   COR   microphyllus   Rosaceae   Ivesia gordonii var.   1800   3500   P   INT   ursinorum   Rosaceae   Ivesia lycopodioides subsp.   3000   4000   P   ENE   Rosaceae   Ivesia lycopodioides subsp.   3000   4000   P   ENE   Rosaceae   Ivesia muirii   2900   4000   P   ENE   Rosaceae   Ivesia muirii   2900   4000   P   ENE   Rosaceae   Ivesia santolinoides   1500   3600   P   ENE   Rosaceae   Ivesia shockleyi   2700   4000   P   ENE   Rosaceae   Ivesia shockleyi   2700   4000   P   ENE   Rosaceae   Potentilla preveri   1500   3700   P   S-C   Rosaceae   Potentilla preveri   1500   3700   P   S-C   Rosaceae   Potentilla glaucophylla var.   2600   3500   P   INT   Rosaceae   Potentilla preveri   2700   3800   P   INT   Rosaceae   Potentilla preveri   2700   3800   P   INT   Rosaceae   Potentilla preveri   2700   3800   P   INT   Rosaceae   Potentilla prevolosericea   2200   3800   P   ENE   Rosaceae   Potentilla prevolosericea   2200   3800   P   INT   Rosaceae   Potentilla prevolosericea   2200   3800   P   ENE   Rosaceae   Ro |                    | alismellus                      |               |                     |       |                            |
| Ranunculaceae   Ranunculas glaberrimus   1200   3600   P   COR   |                    | eschscholtzii                   |               |                     |       |                            |
| Ranunculaceae         Thalictrum alpinum         2900         3700         P         WIE           Ranunculaceae         Thalictrum sparsiflorum         1400         3500         P         COR           Rosaceae         Drymocaulis lactea var.         1800         3700         P         INT           Rosaceae         Drymocaulis pseudorupestris         3200         3900         P         COR           Rosaceae         Drymocaulis pseudorupestris         2300         3500         P         COR           Rosaceae         Iresia gordonii var.         1159         4000         S         COR           mirciphyllus         Invesia gordonii var.         1800         3500         P         INT           Rosaceae         Ivesia lycopodioides subsp.         3000         4000         P         ENE           Rosaceae         Ivesia lycopodioides subsp.         3000         4000         P  | Ranunculaceae      |                                 | 2700          | 4300                | P     | END-CAL                    |
| Ranunculaceae   Thalictrum sparsiflorum   1400   3500   P   COR   Rosaceae   Dasiphora fruticosa   2000   3600   S   WID   Rosaceae   Drymocaulis paeudorupestris   3200   3900   P   COR   10ctea   3700   P   INT   10ctea   3500   P   INT   3500   P   | Ranunculaceae      | Ranunculus glaberrimus          | 1200          | 3600                | P     | CORD                       |
| Ranunculaceae  | Ranunculaceae      | Thalictrum alpinum              | 2900          | 3700                | P     | WIDE                       |
| Rosaceae   Dasiphora fruticosa   2000   3600   S   WIE   Rosaceae   Drymocaulis lactea var.   1800   3700   P   INT   lactea   Rosaceae   Drymocaulis pseudorupestris   3200   3900   P   COR   Rosaceae   Drymocaulis pseudorupestris   2300   3500   P   COR   Rosaceae   Drymocaulis pseudorupestris   2300   3500   P   COR   Rosaceae   Holodiscus discolor var.   1159   4000   S   COR   microphyllus   Rosaceae   Ivesia gordonii var.   1800   3500   P   INT   ursinorum   Rosaceae   Ivesia lycopodioides subsp.   3000   4000   P   ENE   Rosaceae   Ivesia lycopodioides subsp.   3000   4115   P   ENE   scandularis   Rosaceae   Ivesia mirii   2900   4000   P   ENE   Rosaceae   Ivesia mirii   2900   4000   P   ENE   Rosaceae   Ivesia santolinoides   1500   3600   P   ENE   Rosaceae   Ivesia santolinoides   1500   3600   P   ENE   Rosaceae   Ivesia santolinoides   1500   3700   P   S-C   Rosaceae   Potentilla brueeae   1500   3700   P   S-C   Rosaceae   Potentilla bruceae   1200   3700   P   INT   Rosaceae   Potentilla bruceae   1200   3700   P   INT   Rosaceae   Potentilla gracilis var.   2600   3500   P   INT   Rosaceae   Potentilla pensylvanica   2700   3800   P   INT   Rosaceae   Potentilla pensylvanica   2700   3800   P   INT   Rosaceae   Potentilla pensylvanica   2700   3800   P   ENE   Rosaceae   Rosac | Ranunculaceae      |                                 | 1400          | 3500                | P     | CORD                       |
| Rosaceae   |                    |                                 |               |                     |       | WIDE                       |
| Rosaceae   |                    | Drymocaulis lactea var.         |               |                     |       | INT                        |
| Rosaceae   | Rosaceae           | Drymocaulis pseudorupestris     | 3200          | 3900                | P     | CORD                       |
| Rosaceae   | Rosaceae           | Drymocaulis pseudorupestris     | 2300          | 3500                | P     | CORD                       |
| Rosaceae   | Rosaceae           | Holodiscus discolor var.        | 1159          | 4000                | S     | CORD                       |
| Rosaceae   Ivesia lycopodioides subsp.   3000   4115   P   ENE   | Rosaceae           | Ivesia gordonii var.            | 1800          | 3500                | P     | INT                        |
| Rosaceae         Ivesia lycopodioides subsp. scandularis         3000         4115         P         END           Rosaceae         Ivesia muirii         2900         4000         P         END           Rosaceae         Ivesia pygmaea         2700         4000         P         END           Rosaceae         Ivesia santolinoides         1500         3600         P         END           Rosaceae         Ivesia shockleyi         2700         4000         P-MAT         INT           Rosaceae         Potentilla breweri         1500         3700         P         S-C           Rosaceae         Potentilla flabellifolia         1700         3700         P         S-C           Rosaceae         Potentilla bruceae         1200         3700         P         INT           Rosaceae         Potentilla glaucophylla var.         2600         3500         P         INT           Rosaceae         Potentilla gracilis var.         800         3500         P         INT           Rosaceae         Potentilla pensylvanica         2700         3800         P         INT           Rosaceae         Potentilla pensylvanica         2700         3800         P         END   | Rosaceae           |                                 | 3000          | 4000                | P     | END-CAL                    |
| Rosaceae         Ivesia pygmaea         2700         4000         P         ENE           Rosaceae         Ivesia santolinoides         1500         3600         P         ENE           Rosaceae         Ivesia shockleyi         2700         4000         P-MAT         INT           Rosaceae         Potentilla breweri         1500         3700         P         S-C           Rosaceae         Potentilla flabellifolia         1700         3700         P         S-C           Rosaceae         Potentilla bruceae         1200         3700         P         INT           Rosaceae         Potentilla glaucophylla var.         2600         3500         P         WID           Rosaceae         Potentilla gracilis var.         800         3500         P         INT           Rosaceae         Potentilla pessonii         2700         3800         P         INT           Rosaceae         Potentilla pensylvanica         2700         3800         P         ENE           Rosaceae         Potentilla pensylvanica         2700         3800         P         ENE           Rosaceae         Potentilla pensylvanica         2700         3800         P         ENE           Rosace  | Rosaceae           | 2 1                             | 3000          | 4115                | P     | END-CAL                    |
| Rosaceae         Ivesia santolinoides         1500         3600         P         END           Rosaceae         Ivesia shockleyi         2700         4000         P-MAT         INT           Rosaceae         Potentilla breweri         1500         3700         P         S-C           Rosaceae         Potentilla flabellifolia         1700         3700         P         S-C           Rosaceae         Potentilla proteilla glaucophylla var.         2600         3500         P         INT           Rosaceae         Potentilla gracilis var.         800         3500         P         INT           Rosaceae         Potentilla pensulvanica         2700         3800         P         INT           Rosaceae         Potentilla pensylvanica         2700         3800         P         END           Rosaceae         Potentilla pensylvanica         2700         3800         P         END           Rosaceae         Potentilla pensylvanica         2700         3800         P         END           Rosaceae         Potentilla procumbens         1800         3500         P         END           Rosaceae         Sibbaldia procumbens         1820         3700         P         END  | Rosaceae           | Ivesia muirii                   | 2900          | 4000                | P     | END                        |
| Rosaceae         Ivesia santolinoides         1500         3600         P         END           Rosaceae         Ivesia shockleyi         2700         4000         P-MAT         INT           Rosaceae         Potentilla breweri         1500         3700         P         S-C           Rosaceae         Potentilla flabellifolia         1700         3700         P         INT           Rosaceae         Potentilla glaucophylla var.         2600         3500         P         INT           Rosaceae         Potentilla gracilis var.         800         3500         P         INT           Rosaceae         Potentilla pensulvanica         2700         3800         P         INT           Rosaceae         Potentilla pensylvanica         2700         3800         P         END           Rosaceae         Potentilla pseudosericea         3200         4300         P         END           Rosaceae         Potentilla wheeleri         1800         3500         P         END           Rosaceae         Sibbaldia procumbens         1820         3700         P         WID           Rosaceae         Sorbus californica         1200         4300         S         INT <td< td=""><td>Rosaceae</td><td>Ivesia pvgmaea</td><td>2700</td><td>4000</td><td>P</td><td>END</td></td<>  | Rosaceae           | Ivesia pvgmaea                  | 2700          | 4000                | P     | END                        |
| Rosaceae         Ivesia shockleyi         2700         4000         P-MAT         INT           Rosaceae         Potentilla breweri         1500         3700         P         S-C           Rosaceae         Potentilla flabellifolia         1700         3700         P         S-C           Rosaceae         Potentilla bruceae         1200         3700         P         INT           Rosaceae         Potentilla glaucophylla var.         2600         3500         P         INT           Rosaceae         Potentilla gracilis var.         800         3500         P         INT           Rosaceae         Potentilla protentilla pessonii         2700         3800         P         INT           Rosaceae         Potentilla pensylvanica         2700         3800         P         INT           Rosaceae         Potentilla pesudosericea         3200         4300         P         END           Rosaceae         Potentilla wheeleri         1800         3500         P         END           Rosaceae         Potentilla procumbens         1820         3700         P         END           Rosaceae         Sorbus californica         1200         4300         S         INT   | Rosaceae           | 1,0                             |               |                     |       | END-CAL                    |
| Rosaceae         Potentilla breweri         1500         3700         P         S-C           Rosaceae         Potentilla flabellifolia         1700         3700         P         S-C           Rosaceae         Potentilla bruceae         1200         3700         P         INT           Rosaceae         Potentilla glaucophylla var.         2600         3500         P         WID           Rosaceae         Potentilla gracilis var.         800         3500         P         INT           Rosaceae         Potentilla jepsonii         2700         3800         P         INT           Rosaceae         Potentilla pensylvanica         2700         3800         P         WID           Rosaceae         Potentilla pseudosericea         3200         4300         P         END           Rosaceae         Potentilla wheeleri         1800         3500         P         END           Rosaceae         Potentilla procumbens         1820         3700         P         END           Rosaceae         Sorbus californica         1200         4300         S         INT           Rubiaceae         Galium bifolium         1500         3700         A         COR           Rubiacea  |                    |                                 |               | 4000                | P-MAT | INT                        |
| Rosaceae         Potentilla flabellifolia         1700         3700         P         S-C           Rosaceae         Potentilla bruceae         1200         3700         P         INT           Rosaceae         Potentilla glaucophylla var.         2600         3500         P         WIE           Rosaceae         Potentilla gracilis var.         800         3500         P         INT           Rosaceae         Potentilla jepsonii         2700         3800         P         INT           Rosaceae         Potentilla pensylvanica         2700         3800         P         WIE           Rosaceae         Potentilla pensylvanica         2700         3800         P         END           Rosaceae         Potentilla procuntilla pensylvanica         2700         3800         P         END           Rosaceae         Potentilla procuntilla pensylvanica         2700         3800         P         END           Rosaceae         Potentilla procuntilla pensylvanica         1800         3500         P         END           Rosaceae         Potentilla procuntens         1820         3700         P         WIE           Rosaceae         Sorbus californica         1200         4300         S         <  |                    | 2                               |               |                     |       |                            |
| Rosaceae Potentilla bruceae 1200 3700 P INT Rosaceae Potentilla glaucophylla var. 2600 3500 P WID glaucopylla  Rosaceae Potentilla gracilis var. 800 3500 P INT fastigiata  Rosaceae Potentilla jepsonii 2700 3800 P INT Rosaceae Potentilla pensylvanica 2700 3800 P WID Rosaceae Potentilla pseudosericea 3200 4300 P END Rosaceae Potentilla wheeleri 1800 3500 P END Rosaceae Sibbaldia procumbens 1820 3700 P END Rosaceae Sibbaldia procumbens 1820 3700 P WID Rosaceae Sorbus californica 1200 4300 S INT Rubiaceae Galium bifolium 1500 3700 A COR Rubiaceae Galium grayanum var. 1830 3500 P S-C grayanum  Rubiaceae Galium hypotrichium subsp. 3000 4200 P END hypotrichium  Rubiaceae Galium hypotrichium subsp. 2650 3880 P END  |                    |                                 |               |                     |       |                            |
| $\begin{array}{cccccccccccccccccccccccccccccccccccc$   |                    |                                 |               |                     |       |                            |
| $\begin{array}{c ccccccccccccccccccccccccccccccccccc$  |                    |                                 |               |                     | _     | WIDE                       |
| Rosaceae         Potentilla jepsonii         2700         3800         P         INT           Rosaceae         Potentilla pensylvanica         2700         3800         P         WIE           Rosaceae         Potentilla pseudosericea         3200         4300         P         ENE           Rosaceae         Potentilla wheeleri         1800         3500         P         ENE           Rosaceae         Sibbaldia procumbens         1820         3700         P         WIE           Rosaceae         Sorbus californica         1200         4300         S         INT           Rubiaceae         Galium bifolium         1500         3700         A         COR           Rubiaceae         Galium grayanum var.         1830         3500         P         S-C           Rubiaceae         Galium hypotrichium subsp.         3000         4200         P         END           Rubiaceae         Galium hypotrichium subsp.         2650         3880         P         END  |                    | glaucopylla                     |               |                     | P     | INT                        |
| Rosaceae         Potentilla jepsonii         2700         3800         P         INT           Rosaceae         Potentilla pensylvanica         2700         3800         P         WIE           Rosaceae         Potentilla pseudosericea         3200         4300         P         ENE           Rosaceae         Potentilla wheeleri         1800         3500         P         ENE           Rosaceae         Sibbaldia procumbens         1820         3700         P         WIE           Rosaceae         Sorbus californica         1200         4300         S         INT           Rubiaceae         Galium bifolium         1500         3700         A         COR           Rubiaceae         Galium grayanum var.         1830         3500         P         S-C           Rubiaceae         Galium hypotrichium subsp.         3000         4200         P         END           Rubiaceae         Galium hypotrichium subsp.         2650         3880         P         END  |                    |                                 |               |                     |       |                            |
| Rosaceae         Potentilla pensylvanica         2700         3800         P         WIE           Rosaceae         Potentilla pseudosericea         3200         4300         P         ENE           Rosaceae         Potentilla wheeleri         1800         3500         P         ENE           Rosaceae         Sibbaldia procumbens         1820         3700         P         WIE           Rosaceae         Sorbus californica         1200         4300         S         INT           Rubiaceae         Galium bifolium         1500         3700         A         COR           Rubiaceae         Galium grayanum var.         1830         3500         P         S-C           Rubiaceae         Galium hypotrichium subsp.         3000         4200         P         END           Rubiaceae         Galium hypotrichium subsp.         2650         3880         P         END   | Rosaceae           |                                 | 2700          | 3800                | P     | INT                        |
| Rosaceae Potentilla pseudosericea 3200 4300 P END Rosaceae Potentilla wheeleri 1800 3500 P END Rosaceae Sibbaldia procumbens 1820 3700 P WIE Rosaceae Sorbus californica 1200 4300 S INT Rubiaceae Galium bifolium 1500 3700 A COR Rubiaceae Galium grayanum var. 1830 3500 P S-C grayanum Rubiaceae Galium hypotrichium subsp. 3000 4200 P END hypotrichium Rubiaceae Galium hypotrichium subsp. 2650 3880 P END  |                    |                                 |               |                     |       | WIDE                       |
| Rosaceae Potentilla wheeleri 1800 3500 P END Rosaceae Sibbaldia procumbens 1820 3700 P WID Rosaceae Sorbus californica 1200 4300 S INT Rubiaceae Galium bifolium 1500 3700 A COR Rubiaceae Galium grayanum var. 1830 3500 P S-C grayanum Rubiaceae Galium hypotrichium subsp. 3000 4200 P END hypotrichium Rubiaceae Galium hypotrichium subsp. 2650 3880 P END  |                    |                                 |               |                     |       | END-CAL                    |
| Rosaceae         Sibbaldia procumbens         1820         3700         P         WID           Rosaceae         Sorbus californica         1200         4300         S         INT           Rubiaceae         Galium bifolium         1500         3700         A         COR           Rubiaceae         Galium grayanum var.         1830         3500         P         S-C           grayanum         grayanum         T         T         END           Rubiaceae         Galium hypotrichium subsp.         3000         4200         P         END           Rubiaceae         Galium hypotrichium subsp.         2650         3880         P         END   |                    | 4                               |               |                     |       | END-CAL                    |
| Rosaceae Sorbus californica 1200 4300 S INT Rubiaceae Galium bifolium 1500 3700 A COR Rubiaceae Galium grayanum var. 1830 3500 P S-C grayanum  Rubiaceae Galium hypotrichium subsp. 3000 4200 P END hypotrichium  Rubiaceae Galium hypotrichium subsp. 2650 3880 P END   |                    |                                 |               |                     |       | WIDE                       |
| Rubiaceae $Galium\ bifolium$ 1500 3700 A COR Rubiaceae $Galium\ grayanum\ var.$ 1830 3500 P S-C $grayanum$ Rubiaceae $Galium\ hypotrichium\ subsp.$ 3000 4200 P END $hypotrichium\ subsp.$ 2650 3880 P END   |                    |                                 |               |                     |       |                            |
| Rubiaceae $Galium\ grayanum\ var.$ 1830 3500 P S-C $grayanum$ Rubiaceae $Galium\ hypotrichium\ subsp.$ 3000 4200 P END $hypotrichium\ subsp.$ 2650 3880 P END  |                    |                                 |               |                     |       | CORD                       |
| $\begin{array}{cccccccccccccccccccccccccccccccccccc$   |                    |                                 |               |                     |       |                            |
| hypotrichium Rubiaceae Galium hypotrichium subsp. 2650 3880 P END  |                    | grayanum                        |               |                     |       | END-CAL                    |
| 71   |                    | hypotrichium                    |               |                     |       |                            |
|  |                    | subalpinum                      |               |                     |       |                            |
| Salicaceae Salix brachycarpa var. 3200 3500 S COR brachycarpa  | Salicaceae         |                                 | 3200          | 3500                | S     | CORD                       |

APPENDIX 1. CONTINUED.

| Higher level taxon | Specific or infraspecific taxon    | Lower elevation (m) | Upper elevation (m) | Growth<br>form | Biogeographic relationship |
|--------------------|------------------------------------|---------------------|---------------------|----------------|----------------------------|
| Salicaceae         | Salix eastwoodiae                  | 1600                | 3800                | S              | CORD                       |
| Salicaceae         | Salix geyeriana                    | 1450                | 3600                | Š              | CORD                       |
| Salicaceae         | Salix lemmonii                     | 1400                | 3500                | S              | CORD                       |
| Salicaceae         | Salix nivalis                      | 3100                | 3500                | S              | CORD                       |
| Salicaceae         | Salix orestera                     | 1100                | 4000                | S              | S-C                        |
| Salicaceae         | Salix petrophila                   | 1670                | 4000                | S              | CORD                       |
| Salicaceae         | Salix planifolia                   | 2500                | 4000                | S              | WIDE                       |
| Saxifragaceae      | Heuchera rubescens                 | 1000                | 4000                | P              | CORD                       |
| Saxifragaceae      | Lithophragma glabrum               | 0                   | 3750                | P              | CORD                       |
| Saxifragaceae      | Micranthes aprica                  | 1600                | 3600                | P              | CORD                       |
| Saxifragaceae      | Micranthes bryophora               | 1600                | 3500                | P              | CORD                       |
| Saxifragaceae      | Micranthes nidifica                | 1000                | 3500                | P              | CORD                       |
| Saxifragaceae      | Micranthes tolmiei                 | 1980                | 3596                | P              | CORD                       |
| Saxifragaceae      | Pectiantia breweri                 | 1500                | 3500                | P              | S-C                        |
| Saxifragaceae      | Saxifraga hyperborea               | 3000                | 4500                | P              | WIDE                       |
| Valerianaceae      | Valeriana californica              | 1500                | 3700                | P              | INT                        |
| Violaceae          | Viola adunca                       | 0                   | 3570                | P              | WIDE                       |
| Violaceae          | Viola bakeri                       | 900                 | 3800                | P              | INT                        |
| Violaceae          | Viola macloskeyi                   | 609                 | 3600                | P              | WIDE                       |
| Violaceae          | Viola pinetorum subsp. grisea      | 1981                | 3700                | P              | END-CAL                    |
| Violaceae          | Viola purpurea subsp.<br>mesophyta | 1400                | 3598                | P              | END-CAL                    |

APPENDIX 2. Annotated checklist of the flora of the Sierra Nevada with an upper elevational limit of 3300–3499 m. Abbreviations as in Appendix 1. Species names follow Baldwin et al. (2012).

| Higher level taxon | Specific or infraspecific taxon | Lower elevation (m) | Upper elevation (m) | Growth form | Biogeographic relationship |
|--------------------|---------------------------------|---------------------|---------------------|-------------|----------------------------|
| PTERIDOPHYT.       | A                               |                     |                     |             |                            |
| Aspleniaceae       | Asplenium septentrionale        | 2500                | 3350                | P           | WIDE                       |
| Ophioglossaceae    | Botrychium lunaria              | 2300                | 3400                | P           | WIDE                       |
| Pteridaceae        | Adiantum aleuticum              | 0                   | 3400                | P           | WIDE                       |
| Pteridaceae        | Aspidotis densa                 | 100                 | 3400                | P           | CORD                       |
| Pteridaceae        | Cryptogramma acrostichoides     | 1400                | 3400                | P           | INT                        |
| CONIFERAE          |                                 |                     |                     |             |                            |
| Pinaceae           | Pinus monticola                 | 150                 | 3400                | T           | S-C                        |
| MONOCOTS           |                                 |                     |                     |             |                            |
| Alliaceae          | Allium validum                  | 1200                | 3400                | G           | CORD                       |
| Cyperaceae         | Carex abrupta                   | 1200                | 3450                | P-G         | S-C                        |
| Cyperaceae         | Carex aurea                     | 1100                | 3300                | P-G         | WIDE                       |
| Cyperaceae         | Carex buxbaumii                 | 0                   | 3300                | P-G         | WIDE                       |
| Cyperaceae         | Carex davyi                     | 1400                | 3300                | P-G         | S-C                        |
| Cyperaceae         | Carex disperma                  | 1100                | 3400                | P-G         | WIDE                       |
| Cyperaceae         | Carex fissuricola               | 1500                | 3300                | P-G         | CORD                       |
| Cyperaceae         | Carex fracta                    | 250                 | 3300                | P-G         | S-C                        |
| Cyperaceae         | Carex illota                    | 2100                | 3400                | P-G         | CORD                       |
| Cyperaceae         | Carex integra                   | 800                 | 3400                | P-G         | S-C                        |
| Cyperaceae         | Carex microptera                | 1500                | 3400                | P-G         | CORD                       |
| Cyperaceae         | Carex pellita                   | 60                  | 3300                | P-G         | WIDE                       |
| Cyperaceae         | Carex petasata                  | 600                 | 3400                | P-G         | CORD                       |
| Cyperaceae         | Carex preslii                   | 1800                | 3400                | P-G         | CORD                       |
| Cyperaceae         | Carex simulata                  | 0                   | 3300                | P-G         | CORD                       |
| Cyperaceae         | Carex tiogana                   | 3100                | 3350                | P-G         | S-C                        |
| Cyperaceae         | Carex utriculata                | 0                   | 3400                | P-G         | WIDE                       |
| Cyperaceae         | Carex vesicaria                 | 0                   | 3300                | P-G         | WIDE                       |
| Cyperaceae         | Carex whitneyi                  | 1200                | 3400                | P-G         | S-C                        |

|              | APPENDIX 2.                                  | CONTINUED. |               |        |               |
|--------------|--|------------|---------------|--------|---------------|
| Higher level | Specific or                                  | Lower      | Upper         | Growth | Biogeographic |
| taxon        | infraspecific taxon                          |            | elevation (m) | form   | relationship  |
|              | Eleocharis acicularis var. acicularis        | 0          | 3300          | P-G    | WIDE          |
| Cyperaceae   |  |            |               |        |               |
| Cyperaceae   | Eleocharis acicularis var. gracilescens      | 0          | 3300          | P-G    | WIDE          |
| Cyperaceae   | Eleocharis suksdorfiana                      | 0          | 3400          | P-G    | CORD          |
| Cyperaceae   | Eriophorum criniger                          | 2000       | 3350          | P-G    | S-C           |
| Iridaceae    | Iris missouriensis                           | 900        | 3400          | G      | CORD          |
| Juncaceae    | Juncus hemiendytus var. abjectus             | 1400       | 3400          | P-G    | INT           |
| Juncaceae    | Juncus nevadensis subsp. nevadensis          | 1200       | 3300          | P-G    | CORD          |
| Juncaceae    | Luzula parviflora var. parviflora            | 1000       | 3300          | P-G    | WIDE          |
| Liliaceae    | Lilium kelleyanum                            | 2200       | 3300          | G      | END           |
| Orchidaceae  | Platanthera dilatata var. leucostachys       | 0          | 3400          | Ğ      | CORD          |
| Orchidaceae  | Platanthera sparsiflora                      | 100        | 3400          | G      | CORD          |
|              |  |            |               |        |               |
| Orchidaceae  | Spiranthes romanzoffiana                     | 0          | 3300          | P      | WIDE          |
| Poaceae      | Agrostis humilis                             | 1500       | 3350          | P-G    | CORD          |
| Poaceae      | Bromus suksdorfii                            | 1250       | 3300          | P-G    | S-C           |
| Poaceae      | Calamagrostis canadensis var.<br>canadensis  | 1500       | 3400          | P-G    | WIDE          |
| Poaceae      | Calamagrostis canadensis var.<br>langsdorfii | 1500       | 3400          | P-G    | WIDE          |
| Poaceae      | Calamagrostis stricta subsp. inexpansa       | 0          | 3400          | P-G    | WIDE          |
| Poaceae      | Calamagrostis stricta subsp. stricta         | 1500       | 3350          | P-G    | WIDE          |
| Poaceae      | Danthonia intermedia var. intermedia         | 1460       | 3450          | P-G    | WIDE          |
|              |  |            |               |        |               |
| Poaceae      | Elymus trachycaulus subsp.<br>trachycaulus   | 0          | 3400          | P-G    | WIDE          |
| Poaceae      | Hordeum brachyantherum subsp. brachyantherum | 0          | 3400          | P-G    | CORD          |
| Poaceae      | Hordeum brachyantherum subsp. californicum   | 0          | 3400          | P-G    | END-CAL       |
| Poaceae      | Melica bulbosa                               | 0          | 3400          | P-G    | CORD          |
| Poaceae      | Melica stricta                               | 1200       | 3350          | P-G    | INT           |
| Poaceae      | Muhlenbergia filiformis                      | 150        | 3350          | A      | CORD          |
| Poaceae      |  | 1640       | 3420          | P-G    | WIDE          |
|              | Muhlenbergia montana                         |            |               |        |               |
| Poaceae      | Stipa nevadensis                             | 1000       | 3450          | P-G    | CORD          |
| Poaceae      | Stipa occidentalis subsp. californica        | 150        | 3450          | P-G    | CORD          |
| Poaceae      | Stipa occidentalis subsp. occidentalis       | 1200       | 3450          | P-G    | CORD          |
| Poaceae      | Trisetum wolfii                              | 1740       | 3300          | P-G    | CORD          |
| EUDICOTS     |  |            |               |        |               |
| Apiaceae     | Angelica lineariloba                         | 1700       | 3300          | P      | END-CAL       |
| •            |  | 1000       | 3300          | P      | CORD          |
| Apiaceae     | Ligusticum grayi                             |            |               |        |               |
| Apiaceae     | Lomatium torreyi                             | 1100       | 3300          | P      | END           |
| Apiaceae     | Perideridia parishii subsp. latifolia        | 2000       | 3400          | P      | S-C           |
| Asteraceae   | Agoseris parviflora                          | 1400       | 3400          | P      | CORD          |
| Asteraceae   | Artemisia cana subsp. bolanderi              | 1200       | 3300          | S      | S-C           |
| Asteraceae   | Artemisia dracunculus                        | 0          | 3400          | P      | INT           |
| Asteraceae   | Chaenactis douglasii var. alpina             | 3000       | 3400          | P-MAT  | CORD          |
| Asteraceae   | Crepis acuminata                             | 1000       | 3300          | P      | CORD          |
| Asteraceae   | Crepis intermedia                            | 800        | 3300          | P      | CORD          |
| Asteraceae   | Ericameria parryi var. aspera                | 1900       | 3300          | SS     | INT           |
| Asteraceae   | Erigeron barbellulatus                       | 2100       | 3300          | P      | END-CAL       |
| Asteraceae   | Erigeron clokeyi var. pinzliae               | 2200       | 3400          | P      | INT           |
|              |  |            |               | P      |               |
| Asteraceae   | Erigeron coulteri                            | 1900       | 3400          |        | CORD          |
| Asteraceae   | Erigeron elmeri                              | 1300       | 3300          | P      | END           |
| Asteraceae   | Erigeron glacialis var. glacialis            | 1300       | 3400          | P      | CORD          |
| Asteraceae   | Erigeron tener                               | 2300       | 3400          | P-MAT  | CORD          |
| Asteraceae   | Helenium bigelovii                           | 0          | 3400          | P      | S-C           |
| Asteraceae   | Hieracium albiflorum                         | 0          | 3300          | P      | WIDE          |
| Asteraceae   | Hieracium horridum                           | 1350       | 3300          | P      | S-C           |
| Asteraceae   | Hulsea vestita subsp. vestita                | 2400       | 3350          | P      | END           |
| Asteraceae   | Microseris nutans                            | 1000       | 3400          | P      | CORD          |
| Asteraceae   | Nothocalais alpestris                        | 1300       | 3400          | P      | S-C           |
| Asteraceae   | Packera pauciflora                           | 1800       | 3300          | P      | WIDE          |
| Asteraceae   | Senecio triangularis                         | 100        | 3300          | P      | CORD          |
| Asteraceae   | Tetradymia canescens                         | 1000       | 3400          | S      | CORD          |
| Asteraceae   | Tonestus eximius                             | 1800       | 3300          | P      | CORD          |
|              |  |            |               | P      | S-C           |
| Asteraceae   | Wyethia mollis                               | 900        | 3400          | Г      | 5-0           |

Appendix 2. Continued.

|                                   | Appendix 2.  | Continued.          |                     |             |                            |
|-----------------------------------|--|---------------------|---------------------|-------------|----------------------------|
| Higher level taxon                | Specific or infraspecific taxon                                      | Lower elevation (m) | Upper elevation (m) | Growth form | Biogeographic relationship |
| Boraginaceae                      | Cryptanrtha watsonii   | 1250                | 3300                | A           | CORD                       |
| Boraginaceae                      | Cryptantha confertiflora   | 1050                | 3350                | P           | INT                        |
| Boraginaceae                      | Lappula redowskii  | 1300                | 3300                | A           | WIDE                       |
| Boraginaceae                      | Mertensia ciliata  | 1310                | 3380                | P           | S-C                        |
| Boraginaceae                      | Phacelia bicolor   | 700<br>1300         | 3400                | A           | INT                        |
| Boraginaceae                      |  |                     | 3400                | A           | END                        |
| Boraginaceae                      | Phacelia orogenes  | 2060<br>1200        | 3400<br>3400        | A<br>A      | END<br>CORD                |
| Boraginaceae<br>Boraginaceae      |  |                     | 3400                | A           | END-CAL                    |
| Brassicaceae                      | Barbarea orthoceras  | 1200<br>0           | 3400                | B/P         | WIDE                       |
| Brassicaceae                      | Boechera calderi   | 2050                | 3350                | P           | CORD                       |
| Brassicaceae                      | Boechera davidsonii  | 1200                | 3400                | P           | S-C                        |
| Brassicaceae                      | Boechera pygmaea   | 2600                | 3400                | P           | END                        |
| Brassicaceae                      | Boechera stricta   | 1800                | 3400                | P           | CORD                       |
| Brassicaceae                      | Cardamine oligosperma  | 50                  | 3300                | A/B         | CORD                       |
| Brassicaceae                      | Descurainia californica  | 1700                | 3400                | A/B         | CORD                       |
| Brassicaceae                      | Draba asterophora  | 2600                | 3300                | P           | INT                        |
| Brassicaceae                      | Physaria occidentalis  | 600                 | 3350                | P           | INT                        |
| Caprifoliaceae                    | Lonicera conjugialis   | 140                 | 3300                | S           | S-C                        |
| Caprifoliaceae<br>Caryophyllaceae | Symphicarpos rotundifolius var. parishii<br>Ereomogone congesta var. | 1100<br>1200        | 3300<br>3300        | S<br>P      | INT<br>INT                 |
| Caryophynaceae                    | subfrutescens  | 1200                | 3300                |             | INI                        |
| Ericaceae                         | Arctostaphylos patula  | 750                 | 3350                | S           | CORD                       |
| Ericaceae                         | Arctostaphylos uva-ursi  | 2400                | 3300                | S           | WIDE                       |
| Ericaceae                         | Vaccinium caespitosum  | 0                   | 3400                | S           | WIDE                       |
| Ericaceae                         | Vaccinium uliginosum subsp. occidentale                              | 0                   | 3400                | S           | WIDE                       |
| Fabaceae                          | Astragalus bolanderi   | 1400                | 3300                | P           | INT                        |
| Fabaceae                          | Astragalus ravenii   | 3400                | 3450                | P           | END                        |
| Fabaceae                          | Trifolium monanthum subsp. tenerum                                   | 1600                | 3300                | P           | END                        |
| Fagaceae                          | Chrysolepis sempervirens   | 700                 | 3300                | S<br>P      | S-C                        |
| Gentianaceae<br>Gentianaceae      | Frasera puberulenta<br>Gentianopsis simplex                          | 1700<br>1200        | 3400<br>3400        | P<br>P      | END-CAL<br>INT             |
| Grossulariaceae                   | Ribes inerme var. inerme   | 1200                | 3300                | S           | CORD                       |
| Lamiaceae                         | Monardella breweri subsp. lanceolata                                 | 0                   | 3400                | A           | INT                        |
| Montiaceae                        | Claytonia megarhiza  | 2600                | 3300                | P           | CORD                       |
| Montiaceae                        | Lewisia leana  | 1300                | 3350                | P           | S-C                        |
| Onagraceae                        | Chamerion angustifolium subsp. circumvagum                           | 0                   | 3300                | P           | WIDE                       |
| Orobanchaceae                     | Castilleja arachnoidea   | 1300                | 3300                | P           | INT                        |
| Orobanchaceae                     | Castilleja linariifolia  | 1000                | 3350                | P           | INT                        |
| Orobanchaceae                     | Castilleja peirsonii   | 1500                | 3400                | P           | S-C                        |
| Orobanchaceae                     | Castilleja pilosa  | 1200                | 3400                | P           | INT                        |
| Orobanchaceae                     | Castilleja praeterita  | 2200                | 3400                | P           | END                        |
| Orobanchaceae                     | Orobanche fasciculata  | 0                   | 3300                | P           | WIDE                       |
| Papaveraceae                      | Dicentra uniflora  | 1000                | 3300                | P           | CORD                       |
| Phrymaceae                        | Mimulus breweri  | 1200<br>1520        | 3400                | A           | CORD<br>S-C                |
| Phrymaceae<br>Phrymaceae          | Mimulus nanus var. mephiticus<br>Mimulus tilingii                    | 1400                | 3445<br>3400        | A<br>P      | CORD                       |
| Plantaginaceae                    | Penstemon caesius  | 1800                | 3400                | SS          | END-CAL                    |
| Plantaginaceae                    | Veronica americana   | 0                   | 3300                | P           | WIDE                       |
| Polemoniaceae                     | Ipomopsis aggregata subsp. bridgesii                                 | 1800                | 3300                | P           | END                        |
| Polemoniaceae                     | Microsteris gracilis   | 0                   | 3300                | A           | WIDE                       |
| Polemoniaceae                     | Navarretia breweri   | 1000                | 3300                | A           | CORD                       |
| Polemoniaceae                     | Polemonium occidentale subsp. occidentale                            | 900                 | 3300                | P           | WIDE                       |
| Polygonaceae                      | Eriogonum latens   | 2600                | 3400                | P           | <b>END-CAL</b>             |
| Polygonaceae                      | Eriogonum microthecum var. alpinum                                   | 2500                | 3300                | SS          | END-CAL                    |
| Polygonaceae                      | Eriogonum microthecum var. ambiguum                                  |                     | 3300                | SS          | INT                        |
| Polygonaceae                      | Eriogonum saxatile   | 800                 | 3400                | P-MAT       | INT                        |
| Polygonaceae                      | Eriogonum spergulinum var. reddingianum                              | 1300                | 3400                | Α           | INT                        |
| Polygonaceae                      | Eriogonum wrightii var. subscaposum                                  | 200                 | 3400                | P-MAT       | INT                        |

| Higher level taxon | Specific or infraspecific taxon            | Lower elevation (m) | Upper elevation (m) | Growth form  | Biogeographic relationship |
|--------------------|--|---------------------|---------------------|--------------|----------------------------|
| Polygonaceae       | Polygonum polygaloides subsp.<br>kelloggii | 1500                | 3300                | P            | CORD                       |
| Polygonaceae       | Polygonum shastense                        | 2100                | 3400                | P            | S-C                        |
| Potamogetonaceae   | Potamogeton robbinsii                      | 1600                | 3300                | Q            | WIDE                       |
| Primulaceae        | Dodecatheon alpinum                        | 1700                | 3400                | P            | CORD                       |
| Ranunculaceae      | Anemone drummondii                         | 1200                | 3350                | P            | S-C                        |
| Ranunculaceae      | Aquilegia formosa                          | 0                   | 3300                | P            | S-C                        |
| Ranunculaceae      | Caltha leptosepala var. biflora            | 900                 | 3300                | P            | CORD                       |
| Ranunculaceae      | Delphinium nuttallianum                    | 300                 | 3300                | P            | CORD                       |
| Rhamnaceae         | Ceanothus cordulatus                       | 365                 | 3365                | S            | INT                        |
| Rosaceae           | Amelanchier utahensis                      | 200                 | 3400                | S            | INT                        |
| Rosaceae           | Fragaria virginiana                        | 1200                | 3300                | P            | WIDE                       |
| Rosaceae           | Geum macrophyllum var. perincisum          | 1000                | 3300                | P            | WIDE                       |
| Rosaceae           | Horkelia fusca subsp. parviflora           | 1400                | 3300                | P            | CORD                       |
| Rosaceae           | Ivesia gordonii var. alpicola              | 2100                | 3300                | $\mathbf{P}$ | INT                        |
| Rosaceae           | Ivesia saxosa                              | 900                 | 3300                | P            | INT                        |
| Rosaceae           | Rosa woodsii subsp. gratissima             | 800                 | 3400                | S            | INT                        |
| Rosaceae           | Spiraea splendens                          | 548                 | 3400                | S            | S-C                        |
| Salicaceae         | Salix jepsonii                             | 1000                | 3400                | S            | S-C                        |
| Salicaceae         | Salix scouleriana                          | 1                   | 3400                | S            | CORD                       |
| Scrophulariaceae   | Limosella acaulis                          | 0                   | 3300                | A-Q          | WIDE                       |

# A NEW SPECIES OF ASTRAGALUS (FABACEAE) FROM THE WASATCH MOUNTAINS OF UTAH

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### Abstract

Astragalus kelseyae B.L. Corbin, sp. nov. is described as a new species from the central Wasatch Mountains, where it is known from only one small occurrence in Weber County, Utah. It grows in shale talus within the Gambel oak and bigtooth maple shrubland.

Key Words: Astragalus, Fabaceae, rare plant, Utah, Wasatch Mountains.

A new species of *Astragalus* is described from a single population in the foothills of the Wasatch Mountains in Weber County, Utah. This distinctive milkvetch's fruit shape and texture resemble some forms of A. lentiginosus Douglas ex Hooker, but plants differ in having a branching, subterranean caudex, a smaller fruit beak, and generally larger (and fewer) flowers and fruit. Its humistrate growth form and fruit shape resemble A. amblytropis Barneby, but it has firmer fruits and larger flowers. Its large pods are similar to A. megacarpus (Nutt.) A. Gray, and flowers and leaflets are similar to A. beckwithii Torr. & A. Gray, but it differs from both species by having bilocular fruit, shorter leaves, and larger flowers. It differs significantly from each of those species by having dolabriform (malpighian) hairs.

### TAXONOMIC TREATMENT

Astragalus kelseyae B.L. Corbin, sp. nov. (Fig. 1)

— Type: USA, Utah, Weber Co., talus slope above Ogden, T6N, R1W, Sec 26, SLM, 41°14′N, 111°55′W, 1625 m (5340 ft) elevation, 28 May 2010, Beth Lowe Corbin 1292 (holotype: UT; isotypes: NY, CIC, UVSC, to be distributed).

Planta similis *A. lentiginosus* Douglas ex Hooker var. *negundo* S.L. Welsh & N.D. Atwood et *A. amblytropis* Barneby in legumina biloculares et e var. *negundo* in caudices subteranneis elongatis et e ambo in legumina cartilagineis nec chartaceis et pubescentiis dolabriformis differt.

Perennial herb from branched, subterranean, woody caudex branches. Above-ground stems 10–20 cm long, prostrate (Fig. 2). Leaves humistrate, 3.0–5.2 cm long, 1.5–3.0 cm wide, with (5) 7–11 (13) leaflets, the terminal jointed. Leaflets widely elliptical, 8–15 mm long, 6–12 mm wide, tips rounded to obtuse, more or less alternate on the rachis. Leaves and stems silvery green with appressed dolabriform hairs about 0.5–0.8 mm long. Stipules free, triangular, 4–5 mm long. Inflorescence 2–7 flowered, congested, not much

elongating in fruit. Peduncle 13–25 mm; flowering axis 5–10 mm. Calyx 13–16 mm long, 3.5–4.5 mm wide, with narrow teeth 3-4 mm long; calyx pinkish, with light and dark hairs. Petals white, with keel tip slightly purple. Banner 22–26 mm long, 9–11 mm wide, bent midway at about a 120° angle. Wings 19-21 mm long, narrow, slightly cupped. Keel 18-19 mm long. Fruit firm, cartilaginous, fleshy, inflated, bilocular, humistrate, sessile, with narrow and shallow dorsal and ventral grooves, not curved, sometimes red mottled. Fresh pod 35–53 mm long, 18–30 mm thick, 10–17 mm tall (dorsiventrally compressed), with a small beak 3-6 mm long, and short, dolabriform hairs. Dehiscence through the beak, after separation.

Paratypes (topotypes): 19 May 2009 *Beth Lowe Corbin 1235* (BRY), 4 September 2011 *Beth Lowe Corbin 1523* (UTC — to be distributed).

### DISTRIBUTION AND HABITAT

Astragalus kelseyae grows on the lower, west/ southwest-facing slope of the central Wasatch Mountains, on talus openings within Quercus gambelii Nutt. (Gambel oak) and Acer grandidentatum Nutt. (bigtooth maple) shrublands. The talus consists of fine-textured Ophir shale on about 50–60% slope, at about 1625 m elevation. This habitat is just above the old shoreline of the Pleistocene Lake Bonneville. Precipitation is about 51–64 cm (20–25 inches) per year. The site is within the Uinta-Wasatch-Cache National Forest. Astragalus kelseyae is known only from the type locality, where about 150-200 plants were seen in a localized area of about 0.1 ha. It was first found in 2009, and revisited in 2010 and 2011. A popular hiking trail bisects the occurrence, and additional undesignated trails occur within the habitat.

The geology of the Wasatch Mountains is a complicated mix of sedimentary, metamorphic (such as quartzite), and igneous deposits (Yonkee and Lowe 2004). Ophir shale is a Paleozoic era

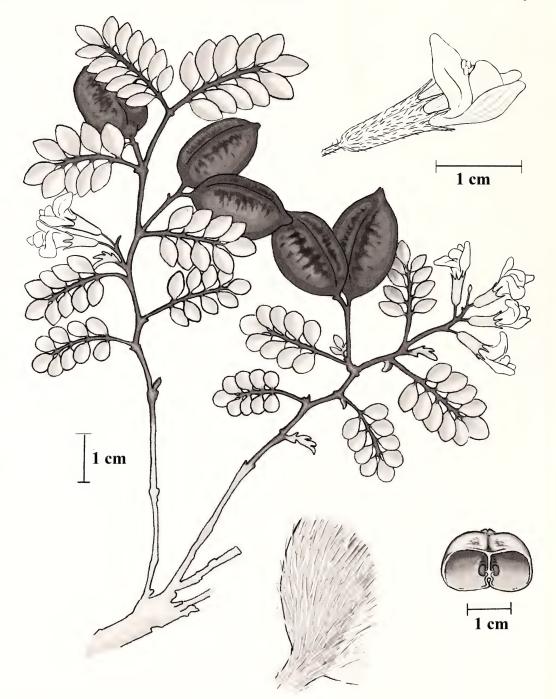


FIG. 1. Astragalus kelseyae habit, flower detail, pod cross section, and leaf hair detail.

sedimentary deposit. Bands of Ophir shale and other similar talus types occur in scattered locations across the Wasatch Front, and additional occurrences of *Astragalus kelseyae* may be found in the future.

The talus microsite is very open, with low cover by associates, including Scutellaria angustifolia

Pursh subsp. micrantha Olmstead, Asclepias asperula (Decne.) Woodson, Apocynum androsaemifolium L., Epilobium canum (Greene) P.H. Raven subsp. garrettii (A. Nelson) P.H. Raven, Hedysarum boreale Nutt., Erysimum capitatum (Douglas) Greene, Eriogonum umbellatum Torr., Pseudoroegneria spicata (Pursh) Á. Löve, Ame-



FIG. 2. Astragalus kelseyae in its shale talus habitat.

lanchier utahensis Koehne, and Phacelia hastata Douglas ex Lehm. Although no weeds occur directly with the Astragalus, several weedy species occur in the vicinity, including Isatis tinctoria L., Linaria dalmatica (L.) Mill., Euphorbia myrsinites L., and Bromus tectorum L., and pose a threat to this species.

### RELATIONSHIPS

Astragalus kelseyae appears to have similarities to A. lentiginosus, A. amblytropis, A. megacarpus, and A. beckwithii, but differs significantly from each (S. Welsh, Brigham Young Univ., personal communication). Its pod resembles A. lentiginosus var. negundo with a large, bilocular fruit, but differs in having a less prominent beak, generally wider fruit, fewer flowers, a branched, subterranean caudex, and dolabriform hairs. It is similar to A. amblytropis in having a subterranean caudex, humistrate stems, leaves, and fruit, and somewhat similar fruit shape, but differs in having firmer pods, larger flowers, free stipules, and dolabriform hairs. It superficially appears similar to A. megacarpus or A. oophorus S. Watson with its large pods, and A. beckwithii with its white flowers, but differs from these species in the section Megacarpi by both its

bilocular fruit and dolabriform hairs. Thus, A. kelseyae differs from each of these species by the presence of dolabriform hairs, and other characteristics as shown in Table 1. The new species' resemblance to A. lentiginosus is likely due to independent parallel evolution, rather than a close relationship; the evolution of a fruit septum (and dolabriform hairs) does not necessarily imply shared ancestry with other species with these characters (J. Alexander, Utah Valley Univ., personal communication). Dolabriform hairs have apparently arisen independently in several sections within genus, but none of the other species with dolabriform hairs have large, bilocular pods, relatively few, large flowers, and prostrate stems. The combination of characteristics present in A. kelseyae appears unique.

Astragalus lentiginosus, with its plethora of varieties, is widespread, including Weber Co., Utah; var. negundo is known from Box Elder Co. (which is adjacent to the north side of Weber Co.) and Millard and Tooele counties (southwest of Weber Co.), Utah, so its range somewhat overlaps that of A. kelseyae (Welsh 2007). Astragalus amblytropis is limited to the vicinity of Challis, in Custer and Lemhi counties, Idaho, some 290 miles north of A. kelseyae (Welsh 2007). Astragalus megacarpus is known from Wyoming

 TABLE 1.
 MORPHOLOGICAL COMPARISON OF ASTRAGALUS KELSEYAE AND SIMILAR SPECIES. Measurements (except A. kelseyae) come from Barneby 1989, Welsh

| Character     | A. kelseyae                     | A. lentiginosus var.<br>negundo       | A. amblytropis                                    | A. megacarpus   | A. beckwithii                         | A. oophorus                                   |
|---------------|---------------------------------|---------------------------------------|---|---|---------------------------------------|---|
| Pubescence    | dolabriform                     | basifixed                             | basifixed   | basifixed   | basifixed                             | basifixed                                     |
| Stem          | humistrate; 10–20<br>cm; caudex | diffuse; 19–32 cm; caudex superficial | humistrate; 10–40 cm; caudex subterranean         | subacaulescent; <5 cm; decumbent to erect; caudex superficial (2) 7–35 (90) cm: | decumbent to erect; (2) 7–35 (90) cm: | decumbent to ascending; 10–25 (30) cm: caudex |
|               | subterranean                    | 1                                     |   |   | caudex superficial                    | superficial                                   |
| Fruit         | large, 3.5-5.3 cm               | smaller, 2.3–3.4 cm long;             | smaller, 2.3-3.4 cm long; smaller, 2-3.5 cm long; | large, $(3.5)$ 4–7 $(7.5)$ cm   | smaller, (1.5) 1.9-3.2                | large, (2) 3–5.5 cm long;                     |
|               | long; inflated;                 | moderately inflated;                  | inflated; papery;                                 | long; inflated; papery;   | (3.7) cm long;                        | inflated; papery;                             |
|               | firm; bilocular;                | stiffly papery; bilocular;            |   | unilocular; rounded at  | narrower; firm;                       | unilocular; rounded                           |
|               | rounded at                      | rounded at base; beak                 | base; beak short                                  | base; beak short  | unilocular; pointed at                | t at base; beak short                         |
|               | base; beak short                | longer                                |   |   | base; beak longer                     |   |
| Flowers       | white; banner                   | whitish (to purple);                  | yellowish; banner 6.4-                            | pink-purple (to white);   | ochroleucous, whitish,                | white to reddish purple;                      |
|               | 22–26 mm;                       | banner 14-21 mm;                      | 8.3 mm; calyx (2.8)                               | banner 16-22 mm;  | to pink-purple;                       | banner 11-23 mm;                              |
|               | calyx 13–16                     | calyx 8–12.5 mm                       | 4-5 mm  | calyx 8.5–14 (16) mm  | banner 16.5-21 mm;                    | calyx 6–12 mm                                 |
|               | mm                              |                                       |   |   | calyx 7–13.5 mm                       |   |
| Inflorescence | 2–7 flowered                    | 5-11 flowered                         | (4) 6–10 (13) flowered                            | 3–5 (8) flowered  | 6–16 flowered                         | (3) 4–10 (14) flowered                        |
| Leaves        | 3-5.2  cm long;  (5)            | (2.5) 4–11 cm long; (7)               | 1-3 (4.5) cm long; 9-13                           | (2) 5–17 cm long;   | (2) 4–15 cm long;                     | (3) 5–15 (21) cm long;                        |
|               | 7–11 (13) leaflets;             | 13–19 leaflets;                       | leaflets; humistrate                              | (7) 9–15 leaflets;  | (7) 11–27 leaflets;                   | 7–25 leaflets;                                |
|               | humistrate                      | spreading                             |   | stiffly erect   | spreading                             | spreading                                     |

(at least 50 miles east of this occurrence), central Utah (about 120 miles south), Nevada, and Colorado, while A. beckwithii occurs in Weber Co. and generally to the west in Utah, and in Idaho, Nevada, Oregon, Washington, and British Columbia (Albee et al. 1988; Welsh et al. 2008; Shultz et al. 2010; USDA 2010). Astragalus oophorus occurs mostly in the southern Great Basin, east into western Colorado, but is also recorded from northwest Utah (Box Elder and Tooele counties) (Welsh et al. 2008; USDA 2010). Thus, the location of A. kelseyae is at the east edge of the ranges of A. lentiginosus var. negundo and A. beckwithii, close to the northern edge of the ranges of A. megacarpus and A. oophorus, and disjunct from A. amblytropis.

Astragalus kelseyae is named in honor of Ann Kelsey, plant collection manager for the University of Utah, with whom I've spent many pleasant field days in the mountains and deserts of Utah.

This plant is of conservation concern because only one occurrence with few individuals is known, and because potential threats exist from trails and invasive weeds.

# KEY TO SIMILAR SPECIES (adapted from Barneby 1989 and Welsh 2007)

- 1. Hairs dolabriform; pods fully bilocular . . . A. kelseyae
- 1'. Hairs basifixed; pods unilocular or bilocular
  - 2. Pods unilocular
    - 3. Pod 1.5–3.7 cm long, valves leathery. . .
    - . . . . . . . . . . . A. beckwithii 3'. Pod (2) 3-6 (7.5) cm long, valves papery
      - 4. Plants subacaulescent, stems 1-
      - 4'. Plants caulescent, stems mostly 5-20 cm long . . . . . . . . . . . . A. oophorus
  - 2'. Pods bilocular
    - 5. Stipules connate; caudex deeply sub-
    - 5'. Stipules free; caudex superficial (near soil surface) . . . . . . . . . . . A. lentiginosus

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# GRIMMIA VAGINULATA, (BRYOPSIDA, GRIMMIACEAE) A NEW SPECIES FROM THE CENTRAL COAST OF CALIFORNIA

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### ABSTRACT

A new California endemic species, **Grimmia vaginulata**, is described and illustrated. It is characterized by its very small size, julaceous habit, immersed capsule on a straight, centrally inserted seta, very large annulus, keeled unistratose leaves, autoicous sexuality, and a large cylindrical ochrea atop the vaginula that sheathes the seta to the base of the capsule. The differentiation and ecology of the new species is discussed.

Key Words: California, endemic moss, **Grimmia vaginulata**, Grimmiaceae, new species, ochrea, vaginula.

In the summer of 2008, prior to the annual meeting of the American Bryological and Lichenological Society, Dale Vitt asked to see *Orthotrichum kellmanii* D. H. Norris, Shevock & Goffinet in the field. During that short trip Dale noticed tiny little plants growing on the same sandstone boulders that supported the *Orthotrichum*. These plants were so scattered and insignificant that they appeared to be immature stems of a small *Grimmia*, and not worth collecting. That impression proved incorrect. Upon microscopic examination, it was immediately obvious that these plants represented a remarkable plant that was unlike any other *Grimmia* in North America.

Chief among the distinguishing characteristics was a transparent extension of the vaginula that extended to the base of the capsule. This extension, known as an ochrea, is not present in any North American Grimmia, and it is not mentioned in any North and Central American Grimmia literature (Flowers 1973; Crum and Anderson 1981; Crum 1994; Hastings and Greven 2007; Muñoz 1999; Muñoz and Allen 2002). To the casual student of the genus, this novel character suggested the possibility of a new genus. That hypothesis was supported by the scattered growth habit. A wider examination of Grimmia was undertaken resulting in the expansion of the North American parameters of the genus.

### TAXONOMY

Grimmia vaginulata Kellman, sp. nov. (Figs. 1A, 1C, 2, 3, 4, 5)—Type: USA, California, Santa Cruz Co., Big Basin Redwoods State Park, on dry vertical walls of calcareous sandstone boulders eroded from the sandstone bedrock in open chaparral, above the Basin Trail and below China Grade Road ca. 1.5 mi. beyond

the northern intersection with SR 236, elev. 685 m, 37°12′40″N, 122°12′42″W, 13 Aug 2008. *Kellman, Vitt, & Shevock 5869* (holotype: CAS).

Species *Grimmia capillata* De Notaris affinis, sed differt ab statura breviore, foliis statu madido vel sicco persistenter julaceis, ochrea cylindracea longiore usque ad prope basem capsulae extendenti differt.

Plants up to 2 mm tall, scattered to very loosely tufted (Fig. 5), simple, or with a short, tightly appressed branch; green when young, tan or white in age; julaceous wet or dry. Lower and perigonial leaves short ovate, 1:1, muticous, increasing in length upwards. Upper stem and perichaetial leaves (Fig. 2B) obovate or elliptical, soft when moist, weakly keeled concave, unistratose throughout, with at least some portion of the leaf margin hyaline, most common at the base and often extending to midleaf or slightly beyond; 1–1.65 mm long  $\times$  0.4–0.75 mm wide (without the awn); the keel is even less pronounced in transverse section, appearing more convex, even tubular, especially on non-sporophytic plants (Fig. 4); apex acute or occasionally slightly acuminate. Basal juxtacostal cells short rectangular with thin to moderately thick, straight; relatively uniform across the base, but outer basal cells often somewhat narrower in 1 to 3 marginal rows. Distal and medial cells decreasing in length gradually from the base to the apex, 1-1.5(2.5):1, 12-16(26) µm long × 7-13 µm wide; rectangular, triangular, or irregularly polygonal, thick-walled, often with some portion of the lumen rounded creating small trigones, not or weakly sinuose; in transverse section plane to slightly bulging. Margins weakly recurved on one or both sides; unistratose. Costa narrow, to 40 μm wide at the base, broadening toward the apex; excurrent in a hyaline, weakly toothed awn shorter than the lamina, decurrent at most 1–2 cells down the margin, and those often projecting

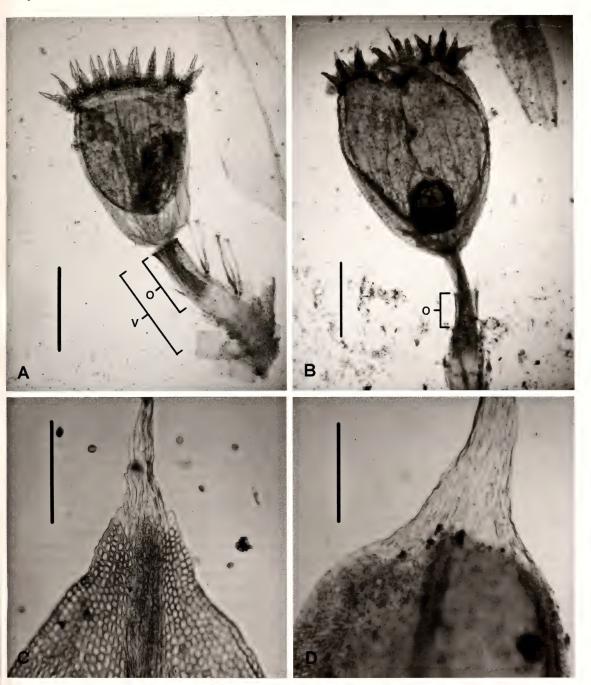


FIG. 1. A. Grimmia vaginulata with leaves stripped exposing the sporophyte. (O) ochrea (V) entire vaginula. Scale bar = 500 μm (from the type); B. G. capillata with leaves stripped exposing the sporophyte. (O) ochrea. Scale bar = 500 μm (Handel-Mazetti 1778, FH: syntype of G. mesopotamica); C. Detail of typical upper leaf apex of G. vaginulata Scale bar = 80 μm; D. Detail of typical upper leaf apex of G. capillata Scale bar = 175 μm.

as short, blunt teeth; costa in transverse section at midleaf with two homogenous rows of cells, 2 cells wide adaxially. Gonioautoicous or cladautoicous. Calyptra irregularly crenate at the base, conical or campanulate, hyaline at the extreme apex and at the base, naked and smooth, just covering the operculum. Vaginula (Fig. 1A),

measured with ochrea, 0.5–0.6 mm long, epidermal cells irregular, about 2–3:1, with very thin, straight walls; distally with a cylindrical ochrea surrounding but not connate to the seta and flaring just below the base of the capsule, 340–430 µm long. Seta straight, attached to the center of the capsule, 0.5 mm long. Capsule immersed

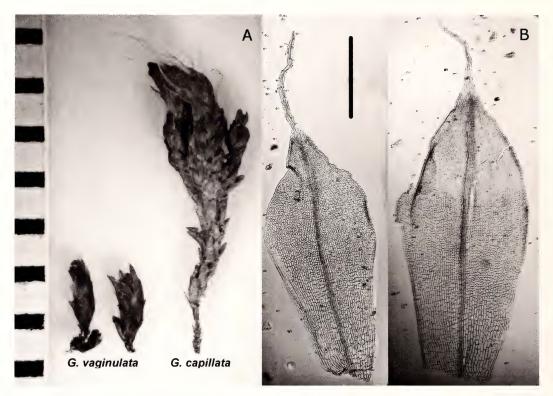


FIG. 2. A. Sporophytic plants of *Grimmia vaginulata* and *G. capillata* showing size difference. Marks are 1 mm apart; B. *G. vaginulata*, two upper and perichaetial leaves. Scale bar = 500 µm.

with only the operculum exposed, irregularly wrinkled when dry, slightly wrinkled when wet, obloid, 0.9 mm long  $\times$  0.6 mm wide, abruptly contracted to the seta. Annulus (Fig. 3) of 3 rows of differentiated, transparent, thick-walled enlarged and elongated cells; remaining on the urn after dehiscence, but gradually falling off in sections. Operculum mammilose to low conical, crenulate to erose at the base. Exothecial cells irregularly rectangular to hexagonal, thin-walled, almost transparent when mature, easily revealing the stalked theca within. Stomata present. Peristome (Fig. 3) of 16 orange-red cribrose-dissected teeth, irregularly divided nearly to the base into 3–4 strongly spiculose filaments, ca. 185 µm long. Spores smooth, 10–13 µm in diameter.

The specific epithet refers to the persistent cylindrical ochrea atop the vaginula, which extends nearly to the base of the capsule.

# IDENTIFICATION AND TAXONOMIC RELATIONSHIPS

Grimmia vaginulata can be distinguished from all other North American Grimmia by the following combination of characters: very small plants that are julaceous wet or dry, upper leaves with hyaline margins, dissected peristome, and a conspicuous and persistent ochrea sheathing the entire seta to just below the base of the capsule.

Grimmia vaginulata resembles G. anodon Bruch & Schimp, and G. plagiopodia Hedw, in leaf shape. However, G. vaginulata remains julaceous wet or dry, and is a much smaller and narrower plant. The straight, centrally inserted seta of G. vaginulata contrasts with the sigmoid, eccentrically inserted seta that characterizes both G. anodon and G. plagiopodia. The extremely dissected peristome resembles G. orbicularis Bruch and G. moxleyi R.S. Williams. Grimmia orbicularis shares the unistratose margins, and the autoicous sexuality with G. vaginulata, but the awns of G. orbicularis are evenly distributed along the stem. Grimmia moxleyi has awns restricted to the upper leaves like G. vaginulata, but the leaf margins are bistratose. Furthermore, both G. orbicularis and G. moxleyi have exserted capsules on arcuate setae. Again, both are much larger than G. vaginulata.

Both gametophytically, and sporophytically, *G. vaginulata* appears most closely related to *G. capillata* De Not., a species scattered around the Mediterranean Sea (Greven 2003). They share the keeled, entirely unistratose lamina with the margins at least somewhat recurved on one or two sides, a costa that broadens in the distal half of the leaf, perichaetial leaves with proximal hyaline areas, and autoicous sexuality. Sporophytically, the two taxa are very close. Lastly, both prefer calcareous substrates. Again, *G. vaginulata* 

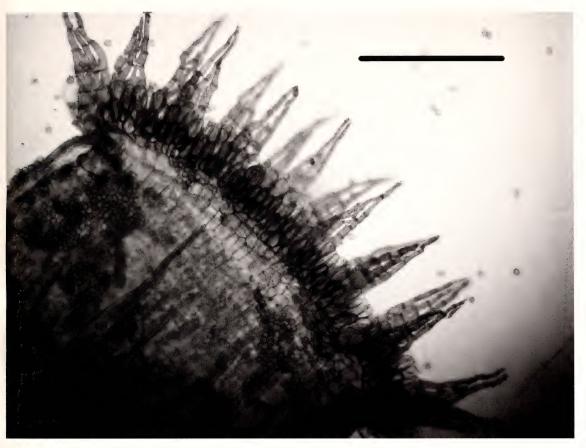


FIG. 3. Detail of annulus and peristome of *Grimmia vaginulata*. Scale bar =  $120 \mu m$ .

is a much smaller plant that stays tightly julaceous wet or dry. My examination of 16 specimens of G. capillata and G. mesopotamica Schiffn. (a synonym of G. capillata fide Muñoz and Pando 2000; Greven 2003) from FU, MUB, and NY show plant size in G. capillata averages around 7 mm, dwarfing G. vaginulata. (Fig. 2A) The dry leaves of G. capillata are erect to erect-patent and are usually strongly keeled. Thus the costae project from the rest of the leaves giving the dry plants a more tumid and textured appearance. When moist, the leaves of G. capillata are at least erect-patent, and are relatively easy to dissect from the stem. The tiny and tightly appressed leaves of G. vaginulata are very difficult to strip for examination without tearing. Leaf size is another point of separation, with the upper stem leaves of G. capillata measuring 2-3 mm long (Cortini Pedrotti 2001; Ignatova and Muñoz 2004), while the much smaller G. vaginulata has leaves with a maximum length of 1.65 mm. In G. *capillata*, the more or less rounded apex (Fig. 1D) is the most commonly hyaline portion of the leaf, while in G. vaginulata, the margins are hyaline, and the apex is acute. There is some small portion at the base of the awn that is hyaline, but at most it is one to two cells down the margin (Fig. 1C).

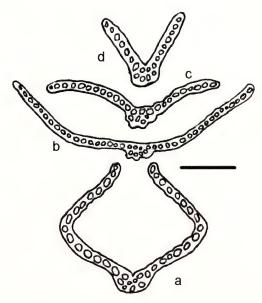


FIG. 4. Drawings of leaf cross sections, *Grimmia vaginulata*; a) leaf from sterile plant taken at midleaf; b, c, d) upper leaf from sporophytic plant. Scale bar =  $100 \mu m$ .



FIG. 5. Grimmia vaginulata. Photograph of growth habit on sandstone.

Although evidence is admittedly sparse, with the only known population being the type, the growth habit of *G. vaginulata* adds another basis for separation. In *G. vaginulata*, the plants are at best loosely associated (Fig. 5), not forming a continuous turf or clump. In *G. capillata*, the plants form dense green mats of sterile plants interspersed with a few fertile plants (Cortini Pedrotti 2001; Greven 2003; Heyn and Herrnstadt 2004; Ignatova and Muñoz 2004). The base of the capsule in *G. capillata* is less abruptly contracted to the seta than is seen in *G. vaginulata*. Lastly, in *G. capillata* the ochrea, while pronounced, extends only half way up the seta, not to the base of the capsule as in *G. vaginulata*. (Figs. 1A, B)

Grimmia pseudoanodon Deguchi, described in 1987 from Peru (Deguchi 1987), is another small autoicous plant (ca 5 mm tall) with immersed sporophytes with a centrally attached, straight seta, and like *G. vaginulata*, the base of its capsule is abruptly contracted. Examination of an isotype from NY, showed several important differences from *G. vaginulata*. First, *G. pseudoanodon* grows in cushions, contrasting the scattered habit of *G.* 

vaginulata. G. pseudoanodon has no peristome, its cauline leaves are not reduced down the stem, being linear to lanceolate and bearing awns to the base of the plant. They are patent to spreading when moist, and are easy to separate from the stem. Similar to G. capillata, the apex of the leaf is hyaline for 15–20 cells, and the awn is often decurrent down the margins of the leaf. Most leaves of G. pseudoanodon show bistratose margins. The vaginula of G. pseudoanodon is extended, demonstrated by the aborted archegonia scattered throughout its length, however, the ochrea is at most represented by a few hyaline flaps at the apex of the vaginula, far from the tube sheathing the seta of G. vaginulata. Interestingly, slight pressure expels the seta from the end of the vaginula, leaving a conical stub at the base of the seta.

### GENERIC TAXONOMY

It is clear that this new plant belongs in the Grimmiaceae. The only other familial possibility is Ptychomitriaceae, and that is ruled out by the

unlobed calyptra. Within Grimmiaceae, other genera can easily be dismissed as well. The large annulus, and the operculum falling independent of the columnella deny placement in Schistidium. Although the cribrose peristome resembles those of both Coscinodon and Jaffueliobryum, and the autoicous sexuality, unistratose lamina and large annulus further support placement in Jaffueliobryum, both genera require a pleated and somewhat sheathing calyptra (Churchill 1987; Hastings 2007; Spence 2007). The calyptra of G. vaginulata is so short that it does not even split or tear during capsule development, sitting instead just atop the operculum. Racomitrium (sensu lato) is ruled out by the lack of sinuosity in the cell walls of the lamina or the vaginula (Deguchi 1978).

Not only can we suggest placement in Grimmia by elimination, but the dramatic characters displayed by G. vaginulata fit well within the limits of variation of plants already in that genus. Deguchi (1978) describes the "Affinis type" annulus as "well differentiated, composed of (2) 3-4 rows of cells, which are thick walled, but transparent, and becoming increasingly larger from the lower to the upper rows. ... Upper rows of cells of the annulus are also removed when the lid falls, but their lower rows usually remain attached to the orifice of the urn, disjoining little by little in the course of time." This is a perfect description of the annulus in G. vaginulata. He attributes this "Affinis type" annulus to "G. affinis, G. anomala, G. apiculata, G. brachydictyon, G. curvata, G. olympica, and G. pilifera." Muñoz (1999) assigns this annulus type to "G. involucrata, G. longirostris, G. poecilostoma, and G. trichophylla" in the introductory section, and 14 other taxa in the species descriptions.

The ochrea is a structure that is poorly understood and has received little taxonomic discussion. Deguchi (1978) makes it clear that the ochrea is only a section of the vaginula, but Magill (1990) defines ochrea as "vaginula, or upper part of vaginula". The haploid vaginula includes cells originating from both the archegonium and the upper part of the stem (Deguchi 1978). Deguchi's proof of this contention is the "occurrence of aborted archegonia at the basal part of the vaginule" (Fig. 1A).

Maier (2002) discusses the vaginula and the ochrea and describes *Grimmia donniana* Sm. ex Spruce with "ochrea broad", with most other species with ochrea "short" or "small". Some species such as *G. orbicularis* (a close relative of the aforementioned *G. moxleyi*) she describes with "vaginula 0.8 mm, with ochrea." Unfortunately, she does not provide illustrations to inform that aspect of her excellent descriptions, nor does she describe how she measures the vaginula. Delgadillo (Universidad Nacional Autónoma de Mexico, personal communication)

wrote "I believe the ochrea is a fairly common feature of the neotropical species of *Grimmia*. It can be demonstrated in *G. americana*, *G. donniana* and *G. elongata*. It is particularly evident in *G. anodon*." But more convincing examples can be found in the persistent ochreae of *G. capillata* and *G. involucrata* Cardot.

Being clear then that this new plant properly belongs in *Grimmia*, it is necessary to at least explore its relationships within the genus. The history of the genus *Grimmia*, s.l, is a tortured and complex story of confused concepts, alternating periods of splitting and lumping, and regional authors describing numerous plants that have been later synonymized in worldwide treatments (Muñoz and Pando 2000; Greven 2003). Deguchi (1978) and Ochyra et al. (2003) both provide a good summary of this nomenclaturally difficult subject. Although Hernández-Maqueda et al. (2008) casts some doubt on Coscinodon, most modern authorities agree on the separation of Jaffueliobryum, Schistidium, and Coscinodon from Grimmia, but there is disagreement whether Grimmia itself requires further subdivision. Ochyra et al. (2003) proposed to split Grimmia into five genera, with each genus corresponding in concept with the subgenera reluctantly suggested by Hastings and Greven (2007). Both systems are rooted in the work of Hagen (1909) and are summarized in Table 1.

Grimmia vaginulata can be ruled out of Gasterogrimmia based on the straight, centrally attached seta. Litoneuron requires 2-stratose, concave leaves with the costa not prominently projecting abaxially: Grimmia vaginulata meets none of these criteria. An expanded Guembelia that included unistratose leaves would fit all characters of G. vaginulata, but if one were to accept the Ochyra et al. (2003) concept of Dryptodon, which includes plants with short straight setae and plicate or wrinkled capsules, then G. vaginulata would belong there. In fact, Ochyra et al. (2003) places G. capillata in Dryptodon.

The difficulty is compounded, however, by statements by various authors suggesting that pairs of plants within *Grimmia s.l.* are closely related, but subsequent authors treat each member of the pair in separate subgenera or genera. For example, G. capillata is often paired with G. crinita Brid. (Greven 2003; Ignatova and Muñoz 2004) and in fact De Notaris (1836, 1838), who first described G. capillata in 1836, reduced it to a variety of G. crinita in 1838, and Maier (2010) reduced G. capillata into synonymy with G. crinita. In this pair, G. crinita is universally placed in Gasterogrimmia (Grimmia sensu Ochyra et al. 2003) but as stated above G. capillata is placed in Dryptodon. These cross subgeneric or generic affinities, as well as the taxa that defy placement within any system, illustrate the

TABLE 1. COMPARISON OF TAXONOMIC TREATMENTS OF GRIMMIA.

| Hastings and Greven (2007) | Ochyra et al. (2003) | Description  |
|----------------------------|----------------------|--|
| Gasterogrimmia             | Grimmia              | Capsules immersed, smooth, seta sigmoid and eccentrically attached to the capsule, leaves 1- or 2-stratose that are concave or concave-keeled.                                     |
| Guembelia                  | Orthogrimmia         | Capsules immersed to exserted,<br>smooth, seta straight and centrally<br>attached to the capsule, leaves<br>mostly 2-stratose and keeled.  |
| Litoneuron                 | Guembelia            | Capsules exserted or emergent,<br>smooth, seta straight and centrally<br>attached to the capsule, leaves 2-<br>stratose that are concave with the<br>costa not prominent dorsally. |
| Rhabdogrimmia              | Dryptodon            | Capsules emergent to exserted, ribbed, seta arcuate and centrally attached to the capsule, leaves mostly 1-stratose (2-stratose at the margins) and keeled.                        |

complexity of *Grimmia s.l.* It is likely that this will only be sorted out by a massive study combining worldwide genetic and morphological data.

The very dramatic and persistent ochrea in G. vaginulata opens the question of the importance of the ochrea in Grimmia taxonomy. Only Maier (2002) and Deguchi (1978) discuss this character. Deguchi briefly mentions the ochrea in his introduction, and then does not use it in his species descriptions. It is ignored in Crum (1994), Muñoz (1999), Cortini Pedrotti (2001), Greven (2003), Ignatova and Muñoz (2004), and Hastings and Greven (2007). Maier (2002) lists G. donniana with ochrea "broad", and G. elatior with ochrea "distinct". Many other species were described with ochrea "small" or the character was ignored altogether. A quick examination of five specimens in CAS annotated by R. Hastings as G. donniana displayed three with no ochrea, one very juvenile capsule with an ochrea already disintegrating, and one specimen with a persistent ochrea about as long as broad at the base of a mature sporophyte. Thus, it seems that this character by itself does not seem to be reliable enough to be useful for separating G. donniana, one of the few taxa that Maier thought had a distinctive ochrea; it is likely, therefore, that the character is not useful beyond the G. capillata-vaginulata group. Nonetheless, further study of such taxa as G. involucrata may show that the ochrea could be an additional character useful for identification

### **ECOLOGY AND DISTRIBUTION**

Grimmia vaginulata has thus far only been found on vertical or underhanging surfaces on calcareous sandstone boulders that have eroded out of less calcareous sandstone bedrock of the Butano Formation. These rocks are scattered through a variably dense chaparral comprised of

Adenostoma fasciculatum Hook. & Arn., Arctostaphylos tomentosa (Pursh.) Lindl., Ceanothus cuneatus (Hook.) Nutt., C. papillosus Torr. & A. Gray, and Eriodictyon californicum Hook. & Arn.. The climate is Mediterranean with moderate but rainy winters, and hot rainless summers (Kellman 2003). The elevation is slightly below 700 meters, placing the site above all but the thickest summer maritime fog. The lack of summer fog keeps these sites very hot and dry until the winter storms arrive.

One of the more peculiar aspects of this very interesting plant is the substrate. With the exception of one recent collection from marble rock (Kellman, Shevock & Lodder 6133 [CAS]) the boulders are also the sole known substrate of Orthotrichum kellmanii, another rare coastal California endemic (Norris et al. 2004). The bedrock was deposited in the Upper Eocene, and is part of the Butano Sandstone Formation (Brabb 1989), but the geologic history of the boulders is not known. Presumably, the rocks were formed and eroded into their rounded shape some time prior to the Eocene deposits that formed the bedrock. In Santa Cruz Co., the Butano Formation is exposed along the western slopes of the highest mountains on the eastern side of the county (Brabb 1989), but the boulders are only present in a small patch in Big Basin Redwoods State Park. There is also a small field of the boulders in southern San Mateo Co., also in Butano State Park. Recently, this same formation with exposed boulders has been found in Monterey Co. within the Ventana Wilderness of the Los Padres National Forest. Orthotrichum kellmanii was collected here although much of the area remains to be surveyed. The new population greatly expanded its range to the south. Although access to these sandstone outcrops was difficult due to hiking through

dense stands of chaparral, the area subsequently burned in the summer of 2008. This area is now among the highest priority sites to survey for *G. vaginulata*—and to document the extent of *Orthotrichum kellmanii* in this area.

Associated bryophytes growing on and around the boulders include *Amphidium californicum* (Hampe ex Müll. Hal.) Broth., *Antitrichia californica* Sull. in Lesq., *Gemmabryum californicum* (Sull.) Spence, *Didymodon vinealis* (Brid.) R.H. Zander, *Tortula muralis* Hedw., *Grimmia torenii* Hastings, *G. pulvinata* (Hedw.) J. E. Smith, *Gymnostomum calcareum* Nees & Hornsch., *G. viridulum* Brid., *Orthotrichum kellmanii*, and *Cephaloziella divaricata* (Sm.) Warnst.

### CONSERVATION

At the type location, *G. vaginulata* has been found on only four out of several hundred boulders, and these fit within a circle of ten meters. It is imperative that no further collections should be made until more populations are found. Additional surveys need to be conducted throughout the highly restricted habitat within the Butano Formation within State Park Lands and a federally designated wilderness area. Even if additional occurrences are discovered, *Grimmia vaginulata* will almost certainly remain a very narrowly restricted endemic that could be adversely impacted by stochastic events.

Even though the chaparral is a fire adapted ecosystem (Schoenherr 1992), the extreme rarity of G. vaginulata leaves open the possibility of fire killing the entire known population. In March of 2009, the author visited the Bonny Doon Ecological Preserve in Santa Cruz Co. Nine months before, in June of 2008, a very hot fire raced through the preserve, where sandstone rocks are scattered through a chaparral very similar to that found at the type location of G. vaginulata. Even in places where the brush was minimal, virtually all bryophytes were killed on the rocks, especially those bryophytes growing on the walls and underhanging surfaces of the rocks. A few mosses and liverworts survived on the tops of a few rocks. Apparently the heat of the fire was trapped under the rocks and then bathed the vertical surfaces, killing all plant life. It is conceivable that thick cushions, or gemmiform plants with densely imbricate leaves could insulate at least some part of a dry moss plant from the heat, but the loose colonies and cylindrical plant form of G. vaginulata offers no such protection.

To date, *G. vaginulata* is known only from the type and in general, taxonomic novelties should not be based on a single specimen, particularly in variable genera such as *Grimmia*. However, this plant's combination of characters, unique to *Grimmia* in North America, along with the conservation implications of its rarity, demand a

full description. Of course, it is always possible that further collections from new locations could alter the concept of G. vaginulata. Of all the characters discussed above, the most likely features to change would be the size and the growth form. It is possible that other populations of G.vaginulata could be composed of larger plants. Arguing against that possibility is the fact that both sterile and fruiting plants exhibit the same size and growth form in the type population. It seems more likely that G. vaginulata could be found growing in turfs or small cushions. However, turf and cushion formation require the survival of the originating stems. There are no subapical innovations in the type population which suggest that this species may be short lived and that individuals die after sexual reproduction.

### ACKNOWLEDGMENTS

I am indebted to Jim Shevock and Dan Norris for teaching me how to do the research necessary to write a paper of this type. They may or may not have been aware that they were teaching me these methods, but an interested student learns as much by observation as by lecture and discussion. I honor their example. I would also like to thank Roxanne Hastings for teaching me the basic understanding of Grimmia, and for a thorough review of this paper resulting in many positive changes. I thank Henk Greven for his review of this paper, and the suggestion to compare Grimmia vaginulata with G. pseudoanodon. David Toren deserves credit for pointing out the illustration of Grimmia mesopotamica in the Bryophyte Flora of Israel that put me onto the similarities of G. vaginulata and G. capillata. Thanks also to Eva Maier, and Claudio Delgadillo, for their insights on the vaginula and ochrea. I also appreciate Claudio Delgadillo and Jesus Muñoz for their helpful comments on an earlier version of this paper. Steve Lodder was invaluable in providing the beautiful photographs. I thank Patricia Eckel for providing the Latin description. I would like to thank the curators of MUB, FH, and NY for the loan of specimens of Grimmia capillata, Grimmia mesopotamica, and Grimmia pseudoanodon, and Deb Trock at CAS who arranged for the loans.

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### **REVIEW**

Introduction to California Chaparral. By RONALD D. QUINN AND STERLING C. KEELEY. 2006. University of California Press, Berkeley, CA. 344 pp. ISBN 9780520219731, \$55.00, hardcover; ISBN 9780520245662, \$21.95, paperback.

In Introduction to California Chaparral, authors Ronald D. Quinn and Sterling C. Keeley condense the beauty and diversity of California's most prominent habitat into a beginners guide suitable for curling up with on the couch or toting along on a hike. The diminutive tome attempts to familiarize the casual observer not only with that superficial "bluish-green blanket gently covering the hills," but also with the dynamic interplay of organisms and underlying ecological processes beneath that oft go largely unseen. It is a monumental task to be sure. To accomplish this task, the authors guide us through the climatic forces that shape the system; the dominant plant, animal and insect species that inhabit it; and other forces such as fire, flooding and urban encroachment that affect it. In addition to describing the chaparral world that modern day adventurers might observe, Quinn and Keeley take us briefly through the history of the chaparral to provide a backdrop of the forces that created such diversity.

In distilling such broad and complex subject matter, the authors only stumble in perhaps the most complex of chaparral arenas: wildfire. Dedicating roughly 1/6 of the book specifically to fire and regularly referring to it throughout the rest, the authors succeed in divulging most of the issues surrounding fire in chaparral. However, their attempt at presenting those issues together in a cohesive and coherent whole falls short and proves dangerously misleading. Notwithstanding, the authors bring hundreds of years of scientific discovery, field observation and a love of California's defining ecosystem into an accessible and enjoyable guide for the masses.

This attractive collection consists of 302 pages of text, color photos, black and white diagrams, plus a glossary and reference section for those who wish to dig deeper. All this is printed on thick, sturdy pages that will no doubt survive the jostles of the many hikes it is sure to inspire.

Quinn and Keeley, Professors of biological science and botany, respectively, draw on a wide range of sources and personal research in compiling this guide. They use these sources to paint a colorful mural of wood-rat nests, heat-seeking fire beetles, iridescent hummingbirds and an impressive array of plants that have managed to survive eons of yearly drought and occasional wildfire. The descriptions are presented at an

accessible level of detail for its intended audience. Plant and animal common names are provided in conjunction with their scientific equivalents. Throughout the guide, the particular adaptations that help chaparral plants and animals survive this difficult environment, i.e., the very features that make them uniquely chaparralian, are highlighted. Reference especially is often given to a particular species' relationship to fire. The authors provide not only colorful descriptions but interesting facts that keep even the most hardened urbanite engaged.

Unfortunately, colorful language occasionally gives way to literary excess. The authors too often employ personification, especially with respect to plant characteristics, that can undermine the integrity of the data presented.

An example on the innocuous end of the spectrum involves a species of monkey flower, Mimulus aurantiacus. The authors describe the unique stigma that assumes a closed position when pollinated or even just touched by an insect or animal. The authors then claim that in so doing the plants "advertise their status" as pollinated or not, presumably giving pollinators the plant kingdom's equivalent of a wedding ring to wouldbe suitors. Does a closed stigma make it more likely that pollinators will move to another flower, or is there some other evolutionary incentive for the stigma closing? It's a question the authors don't address, nor is the conclusion supported with cited research. In this case, it's an admittedly harmless conclusion.

The authors' phrasing becomes critically dangerous with regard to fire. The first example comes in the punctuating sentence of the introductory paragraphs to the fire section. It reads: "In short, where there is chaparral, there is fire." While this may technically be true, it is misleading. Where there is chaparral there is going to be fire. But where there are grasslands there is fire. Where there are conifer forests there is fire. In other words, the presence of fire in chaparral is not due to something inherent in the plant community. Rather, where there is chaparral there is a Mediterranean climate and where there is a Mediterranean climate (or any other dry climate with enough moisture to sustain vegetative growth) and an ignition source there will be fire, regardless of vegetation type.

The phrase implies that chaparral fosters a fire environment rather than the more accurate paradigm that chaparral species exist because they are able to survive infrequent fires. The result of the authors' approach is a subtle perpetuation of the oft repeated and poorly applied concept that chaparral needs to burn. As the authors themselves state, certain species do produce seeds that require fire cues to germinate. On the other hand, we know chaparral stands existing for more than a century without fire are perfectly healthy systems and if chaparral stands burn too frequently they can be converted to non-native grasslands. Extrapolating this dichotomy is a tightrope that the authors have difficulty walking.

The most prominent example comes in their "Living with the Chaparral" chapter. In it, the authors describe the merits of prescribed fire and clearing fuel breaks, offering them as effective means to reduce mature chaparral and thus reduce the hazards fire presents to humans. Young chaparral, they suggest, burns less intensely and cuts off the fuel supply, extinguishing fires. Later, not as a counterpoint but as a discrete section, they explain that extreme weather conditions drive fires right through fuel breaks and fuel-age mosaics presumably negating the value of such "barriers".

Further on, the intrinsic watershed value of mature chaparral stands is described in detail. The authors explain that "mature chaparral acts as a sponge" retaining rainfall in the soil and aquifers beneath. Without a mature chaparral and root system, water skims off the soil surface creating disastrous debris flows and leaving no water behind for the ecosystem. That the previously advocated prescribed burning and man-made fuel breaks destroy this important "sponge" mechanism is a conclusion never fully reconciled by the authors.

In truth, land management with respect to wildfire, watershed values, and protecting lives and property is very much a balancing act that few, if any, have yet to master. It is perhaps unfair then to expect the authors to provide solutions to this dilemma. Rather than offer a cohesive recommendation, the authors drop all the issues in our lap and leave us to sort them out. It is a safe approach. Nevertheless, since this work appears to imply that mature chaparral is a threat to humans rather than the other way around, it will likely draw ire from some ecologists and conservationists. And in that sense it is perplexing to find the text demonizing an ecosystem because it can be inconvenient to humans. While perhaps not packaged in the most ideal manner, the authors at least conclude the wildfire section with a plea for humans to take responsibility for their urban planning practices to avoid further losses.

Muddled fire issues aside, this is an "Introduction to California Chaparral" and in that sense it serves its purpose well. Quinn and Keeley's work is a celebration of a unique and teeming habitat. To the reader unfamiliar with that amorphous blanket of shrubs covering the hillsides outside their car windows, Introduction to California Chaparral provides a comprehensive glimpse into that complex habitat. Where the authors particularly shine is in capturing the sheer diversity and dynamic drama found within the often impenetrable chaparral canopy. Were the reader to carry this guide out into the field with them they would likely recognize many more twitters, rustles and floral displays than ever before. Ultimately, creating that connection to the natural environment is the greatest gift any environmental author can bestow upon a reader. In Introduction to California Chaparral Quinn and Keeley are likely to succeed in doing so many times over.

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### **CALIFORNIA**

PORPHYRA SUBORBICULATA Kjellman 1897:10–13 (BANGIACEAE).—Marin Co., epizoic on barnacles attached to pilings in the upper intertidal at Nick's Cove, Tomales Bay, 38°11′57.42″N, 122°55′16.40″W, thalli sterile and fertile, 12 May 2011, *J. R. Hughey s.n.* (UC 1966687, UC 1966688) and 20 July 2011, *J. R. Hughey s.n.* (UC 1966689).

Previous knowledge. Porphyra suborbiculata is naturally distributed throughout Asia (type locality: Gotoretto, Nagasaki Prefecture, Japan (Silva et al. 1996) and reportedly also occurs naturally in the Indian Ocean, Australia, and New Zealand (Broom et al. 2002). However, based on recent molecular evidence some P. suborbiculata from Australia and New Zealand, as well as North America (Mexico and the Atlantic coast of North America) represent introduced populations (Broom et al. 2002; Klein et al. 2003; Neefus et al. 2008). The occurrence of this seaweed in areas associated with increased shipping activity suggest that its numerous introductions were the result of hitchhikings on the hulls of seagoing vessels (Broom et al. 2002). In the eastern Pacific, P. suborbiculata was first collected in 1985 from Baja California, Mexico (Aguilar-Rosas and Aguilar-Rosas 2003). Although P. suborbiculata shows some variation in morphology, it is generally characterized as being a relatively small (0.5-4 cm in diameter), monostromatic alga, with brownish red to pink, or bronze and violet colored blades that are ovate to cordate or reniform in shape (Broom et al. 2002; Aguilar-Rosas and Aguilar-Rosas 2003; Neefus et al. 2008).

Significance. First report of P. suborbiculata in California. The gametophytic thalli collected from Tomales Bay are in agreement with descriptions and illustrations of this species. Specimens from California are cordate at the base, and ovate to deeply reniform in shape. The margins are slightly ruffled and appear dentate to the unaided eye. Under microscopic examination thalli show the diagnostic marginal teeth. The blade color is reddish-brown in spring and steel greenish in summer, and fronds are more or less equal in width and height, measuring to 1.8 cm. Spot checks for this alga at Marshall and Marconi failed to yield additional specimens. Identification of this invasive species was confirmed using rbcL (GenBank JN413680) and ITS-1 (GenBank JN413679) DNA sequences. The rbcL sequence was identical to two sequences from Japan (Kanagawa, Yokosuka, Sajima and Yamaguchi, Shimonoseki, Tsunoshima) and differed from others in the database by 2 or more bp. The ITS-1 sequence was identical to fifteen other sequences deposited in GenBank representing populations from around the world. Since the rbcL sequence generated for P. suborbiculata from Tomales Bay matches specimens from Japan and the ITS-1 sequence is identical to other invasive populations of this species from Australia, Baja California, New Zealand, and the western Atlantic, it is concluded that the population from California is also

the result of an introductory event. In Tomales Bay, *P. suborbiculata* joins a list of five other non-native algae: *Caulacanthus ustulatus* (Turner) Kützing, *Codium fragile* subsp. *tomentosoides* (van Goor) P. C. Silva, *Gelidium vagum* Okamura, *Lomentaria hakodatensis* Yendo, and *Sargassum muticum* (Yendo) Fensholt (C. K. Kjeldsen, Sonoma State University, unpublished data; Hughey 1995; Hughey et al. 1996). The mariculture of oysters in Tomales Bay began around 1907 (Barrett 1963), and oysters are the likely vector for the introduction of *P. suborbiculata* in the bay.

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### CALIFORNIA

SEQUOIADENDRON GIGANTEUM (Lindl.) J. Buchholz (CUPRESSACEAE) (giant sequoia, big tree, or Sierra redwood).—Riverside Co., northwestern San Jacinto Mts., northeast of HW 243 about 18 highway km NW of Idyllwild, in the southern unit of the San Bernardino National Forest, on the northwestern flank of Black Mt. along both sides adjacent to and well back from the Black Mountain Trail, from upper Hall Canyon, through the sloping plateau or saddle near the westerly ridge, and into the final switchback ascent to the summit (elev. 2369 m). Species seen from 2036 to 2236 m elev. in mixed-conifer forest (Lower Montane Coniferous Forest) on sandy granitic soil; associates include: Abies concolor, Pinus coulteri, P. ponderosa var. pacifica, and Quercus chrysolepis dominant at lower elevations; P. jeffreyi and P. lambertiana dominant at higher elevations; Calocedrus decurrens, P. flexilis, and Ribes nevadense throughout most of area; 1 May 2009.

Collections (vouchers to be deposited at RSA, UC, and UCR). Tree DBH 65 cm, sterile, just left (as ascending) of trail on slope by large trunk lying across trail, N33 49.540, W116 45.977, 2036 m elev., R. Schmid & M. Schmid 2009-1; tree with abundant male cones, right (as ascending) of trail on slope covered with Pteridium aquilinum and near drainage (Indian Creek) with Alnus rhombifolia, N33 49.579, W116 45.891, 2066.5 m elev., R. Schmid & M. Schmid 2009-2; mature seed cones with opened cone scales and dislodged seeds, plus mix of sandy granitic soil and sparse duff, along Black Mountain Trail above drainage (Indian Creek) and below sloping plateau or saddle, ca. 2070 m elev., R. Schmid & M. Schmid 2009-4; tree DBH 20 cm, with medium-sized female cones, right (as ascending) side of trail in flat open area, N33 49.607, W116 45.854, 2093 m elev., R. Schmid & M. Schmid 2009-5; tree ca. 5.5 m high, with many, very large, immature female cones, just left (as ascending) of trail in flat open area, N33 49.713, W116 45.773; 2144 m elev., R. Schmid & M. Schmid 2009-6.

In addition to these collections made on 1 May 2009, we did a GPS census in the vicinity of the Black Mountain Trail, starting in upper Hall Canyon. The census revealed both in the canyon and upslope beyond it at least 157 individuals from 2036 to 2236 m elev. (ca. 0.7 km linear distance, ca. 0.1 km<sup>2</sup>), plus an outlier sapling 450 m distant at 2361 m elev. near the summit of Black Mt. (2369 m). Our set of plots involved four groups at progressively higher elevations: (1) at the head of Indian Creek in the drainage (including vouchers 2009-1 and 2009-2); (2) on the slope coming out of the drainage (including voucher 2009-4); (3) at the sloping plateau or saddle (including vouchers 2009-5 and 2009-6); (4) on the northwest-facing slope closer to the summit. This species alien to southern California is regenerating prolifically on Black Mt., as revealed by multiple age classes, from seedlings and saplings (juveniles) about 20-60 cm tall to trees over 6 m tall, about 40 years old, and reproductively mature.

Previous knowledge. The monotypic California endemic Sequoiadendron giganteum is native to the western slope of the Sierra Nevada, where it occurs in

isolated groves in mixed-conifer forest (Lower Montane Coniferous Forest) between 825 and 2700 m elev. The 67 groves are mostly of very restricted extent and/or threatened. They occur in a narrow strip measuring about 395 km long (northwest-southeast) and 19–21 km at the widest points (east-west) and extending over seven counties from southern Placer Co. southeasterly to southern Tulare Co. (Flint 2002; Willard 2000).

This species has been extensively planted in California as an ornamental, as part of afforestation attempts, and as reforestation efforts, especially post-fire revegetation ones. For example, Burns and Sauer (1992) noted that 22,900 seedlings of S. giganteum were planted in southern California in the San Gabriel Mts. alone, but neither this species nor 44 other alien conifer species planted there as part of afforestation projects "are invading adjacent natural habitats" (p. 49). However, Rogers (1986: p. 33) wrote: "On the San Bernardino [National Forest] about 5000 to 10,000 seedlings are planted each year, and at least one instance of natural regeneration from some of the early plantings has been observed." Rogers's "one instance" may well be the introduction of S. giganteum after the Aug. 1974 fire in Hall Canyon (Keeler-Wolf 1990; Cheng 2004) and its subsequent naturalization on Black Mt., which is the subject of the present preliminary report. Our extensive analysis of the print and Internet literature for the floristics and ecology of southern California suggests S. giganteum is possibly also naturalized in the San Gabriel Mts. of Los Angeles Co. and southwestern San Bernardino Co., and in the San Bernardino Mts. of San Bernardino Co.

Significance. First report and collections for Riverside Co. and the San Jacinto Mts. (see the database of the Consortium of California Herbaria, http://ucjeps.berkeley.edu/consortium). More importantly, first documented record for naturalization of this Sierra-Nevada endemic species in montane southern California. State and regional floras for California should acknowledge in their keys and descriptions such naturalizations. Details of these findings will be published elsewhere (Schmid and Schmid in press).

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#### Colorado

DRABA WEBERI R.A. Price & Rollins (BRASSICA-CEAE).—Park Co., Middle Fork of the South Platte, near Magnolia Mill, Pike National Forest, in mossy depressions on north side of granite boulder, 10 plants in flower and fruit, at 39.36112°N, 106.09013°W, 3,398 m elev., 20 July 2010, Bernadette Kuhn 7927a and 7927b, along with Gina Glenne, Sheila Lamb, Alicia Langton, Ellen Mayo, Steve Olson, and Jeff Sprovkin (MO). Dr. Ihsan Al-Shehbaz verified the identification.

Previous knowledge. Global distribution is limited to the type locality in the Monte Cristo Creek drainage, below the Upper Blue Lake Reservoir Dam, on the west side of Continental Divide, Summit County, Colorado. As described in the original publication (Price and Rollins 1991) the holotype (Price #464) was collected from "crevices of rocks beside cascades, amid rocks at edge of stream". The type locality was described by Price as containing "perhaps 100 individuals", and in 2009, 81 individuals were reported present at the site (Colorado Natural Heritage Program 2011). All individuals documented are on private land owned and operated by Colorado Springs Utility, though the site is surrounded by National Forest System lands (Decker 2006).

Significance. Second documented occurrence. For twenty years botanists have been searching for another occurrence outside the species' type locality. Our collection, located 2.8 km to the south, expands the known distribution of *D. weberi* to another county (Park), and to the east side of the Continental Divide. In addition, it confirms the long-suspected presence of *D. weberi* on National Forest System land. This finding, along with the recent addition of *D. weberi* to the

USDA Forest Service Sensitive List, may present new opportunities for the management and conservation of this extremely rare Colorado endemic (USDA Forest Service 2011).

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### MEXICO

ANEMONE TUBEROSA Rydb. (RANUNCULA-CEAE).—Baja California, Municipio of Ensenada, Ejido Nativos del Valle heading W to Santo Tomas, 31.42561°N, 116.34858°W (WGS 84), 434 m/1428 ft, 26 March 2010, Sula Vanderplank, Sean Lahmeyer, Ben Wilder and Karen Zimmerman 100326-29 (RSA), Less than 100 plants observed growing with Zigadenus sp. on N-facing side of a steep limestone outcrop. Most plants in full flower.

Previous knowledge. The general habitat of this species is given by Dutton et al. (1997), in the Flora of North America, as from rocky slopes and stream sides 800-2500 m. It is known from desert regions of the southwestern USA (CA, NM, NV, TX, UT) and NW Mexico (Baja California, Sonora), and has been well documented within the Sonoran and Mojave deserts: Wiggins (1980) reports it from the western edge of the Colorado Desert and the eastern Mojave Desert; Wilken (1993) gives the range in California as eastern Desert Mountains; 900-1900 m; Munz (1974) reports elevations of 3000-5,000 ft (914-1520 m), in Joshua Tree Woodland and Pinyon-Juniper Woodland, western edge of the Colorado Desert, eastern Mojave Desert. The westernmost known collections for this taxon in California are from the southern Cuyamaca Mtns., near the southwestern end of Poser Mtn, March 19 1995, Jeri Hirshberg 253 (RSA) 60 km from the Pacific coast; and the Laguna Mountains, below Desert View, 06 April 1939, A. J. Stover 245 (SD), 80 km from the Pacific coast (CCH 2011). In Arizona, Kearney and Pebbles (1951) report elevations of 2,500–5000 ft (760– 1520 m). In Mexico, the two Baja California collections closest to the Pacific Ocean are both 50 km inland (30– 45 km from the Gulf of California to the east) in the central desert, close to the narrowest part of the peninsula: summit of volcanic hill at top of Jaraguay Grade, 24 Feb 1973, Reid Moran 20248 (SD), elev. 875 m, (the lowest documented elevation for this species in the state); Sierra San Borja, summit of Cerro la Chona, 19 Mar 1966, Reid Moran 12782 (SD), 1450 m (San Diego Natural History Museum 2011). There are a small number of California specimens from ~400 m elev., all from a small area within the Whipple Mountains, on the border with Arizona (CCH).

Significance. First collection of this species west of the peninsular ranges and inside the California Floristic Province. This collection represents a range extension of ca. 70 km west from the peninsular ranges, and is the most coastal collection documented to date, being just 15 km (9 mi) from the Pacific Ocean. The elevation is the lowest recorded in Baja California, and is near the lowest elevation recorded for the species anywhere. Further investigation of the foothills surrounding this site may help determine if this small population is indeed isolated from the core range, perhaps as a result of the unusual habitat provided by the limestone outcrop.

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